Diet of *Cercopithecus nictitans*| and investigation into its potential to act as a surrogate disperser in disturbed Afromontane forests.

A thesis submitted in partial fulfilment of the requirements for the Degree of Master of Science in Zoology at the University of Canterbury

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Abstract

Increasingly, the world's tropical forest are under threat. Climate change and a booming global population means that deforestation and degradation are occurring at alarming rates. Measures to combat this are often costly and suffer from the need of continued human input and monitoring. Encouraging or creating plant-animal mutualisms which encourage regeneration can create a positive feedback loop perpetuating regeneration at little or no cost. In this study I investigated the diet of three troops of *Cercopithecus nictitans* living in Ngel Nyaki Nigeria over three years to investigate how they could potentially help regenerate this fragmented and degraded. A particular threat to this forest is the loss of larger bodied disperser. I wished to determine if *C. nictitans* ecological flexibility would allow it to fill such a role. As it is a largely understudied species, I first determined its diet comparing years of differing availability to ensure I captured the full breadth of their diet. I found that *C. nictitans* ate a varied diet, which was responsive to different causes of scarcity. Males and females ate different diets, with females eating more leaves and less fruit. During periods of extreme scarcity *C. nictitans* increased its consumption of arthropods, a finding which suggests it may predate on less seeds than previously thought. I then used this data to investigate indicators of effective seed dispersal; overlap, dietary niche and preference. I found mixed results, with findings suggesting that *C. nictitans* eats a large amount of large fruited species but that which species it ate was variable. Investigations into selection for seed characters found a constant preference for fruit with many, small, oval seeds, however as food availability decreased *C. nictatans* showed an increase in consumption of fruit with one, large, oval seed. Which has positive implications for its role as an effective seed disperser at Ngel Nyaki. Finally, I investigated fallback foods for *C. nictitans* to aid in its conservation, and help better understand variation in diet. I however failed to find any fallback foods. Overall this study suggests that *C. nictitans* eats a flexible diet, involving many large fruited species. Its diet is highly variable, so it seems unlikely it is dispersing many seed effectively from the perspective of the plant species. These same characteristics may make it an effective disperser from the perspective of the forest. To determine this requires more study, focusing on species indentified in the current study.

1| Introduction

Habitat loss and fragmentation

Habitat loss and fragmentation are amongst the leading causes of species loss globally (Wilcox and Murphy 1985, Krauss et al. 2010, Hanski 2011, Laurance et al. 2012). This is especially true in tropical forests. Tropical forests experience the highest rates of loss of any forest type, and are home to two-thirds of all species (Pimm and Raven 2000). Tropical forests are under threat from a range of factors including fire, logging, hunting, and conversion to agriculture (Chapman and Peres 2001, Balcomb and Chapman 2003, Isabirye-Basuta and Lwanga 2008). These factors lead to deforestation, fragmentation and degradation, which in turn lead to species loss (Chapman and Lambert 2000, Balcomb and Chapman 2003, Marsh and Loiselle 2003). Though some areas, such as the well-documented example of Brazil have seen a decrease in rates of forest decline (Nepstad et al. 2009, Blaser 2011, Hansen et al. 2013), this is offset by increased rates of deforestation elsewhere resulting in an annual global rate of loss of 0.49% between 1990 and 2010 (Achard et al. 2014). This estimate is based off satellite images and does not account for forest type, therefore includes gains due to plantation forest. Subsequently rates of loss of primary forest may be higher. Furthermore, the rate of loss in individual countries can be much higher. For instance Nigeria is estimated to lose on average 4% of its forests per annum between 2005 and 2010 (Blaser 2011).

These threats not only have direct negative effects on plant populations, but also indirect impacts on wildlife populations which rely on the plant populations for survival (Pimm and Raven 2000, Brooks et al. 2002, Fahrig 2003). Large animal species, such as primates, in particular have a high risk of extinction (Chapman and Peres 2001, Cardillo et al. 2005). This is believed to be due to both intrinsic and environmental factors; large bodied species tend to live at lower population densities, have a lower intrinsic rate of population increase, and be subject to higher hunting pressure (Cardillo et al. 2005). Certain orders may at particular risk, including primates around 80% of which live in highly threatened tropical forests (Tutin and White 1998). Declines or loss of wildlife species are concerning in their own right, with at risk species worthy of study to aid conservation. Loss of large bodied species in particular, can in turn also impact on plant populations through the loss of ecosystem processes such as seed dispersal, thus resulting in a negative feedback loop (Chapman and Onderdonk 1998).

As with other primate species, humans are reliant on forests for the ecosystem services they provide such as provision of food, wood and medicine, watershed protection, and carbon sequestration (Lamb et al. 2005, Asongu and Jingwa 2012, Linard et al. 2012). This is especially true in poor rural communities in the tropics, where forests may be the primary source of food and income, and where currently at least 300 million people depend on degraded or secondary forest (Lamb et al. 2005). However this reliance puts forests at risk with both increased deforestation for conversion of land for farming, and logging for timber and fuel wood (Asongu and Jingwa 2012). The rate of deforestation in Africa has been shown to be correlated with the rate of population growth, the pace of which continues to increase (Jha and Bawa 2006, DeFries et al. 2010). Conservation of remaining forest and regeneration of

lost forest is therefore not only important due to the intrinsic value for the forest and its wildlife, but also for the services and resources forests provide for human populations that live in or nearby. Conservation of seed dispersing wildlife species, such as primates, can help facilitate this as it can prevent forests experiencing reduced regeneration (Chapman and Peres 2001).

Seed dispersal is crucial for the survival of forests, this may be especially true for forests which have experienced fragmentation (Terborgh et al. 2008, Ruxton and Schaefer 2012). In these landscapes, seed dispersal is a strong influence on both species persistence and recovery post-disturbance (McConkey et al. 2012). Larger seeded fruit species often experience reduced dispersal in fragments compared to smaller seeded species (Cramer et al. 2007). For animal dispersed species this is likely due to a decrease in the number of large bodied frugivores able to handle the seeds (Moran et al. 2004, Ruxton and Schaefer 2012). Due to its importance and varying effect on plant species, seed dispersal needs to be considered and incorporated into forest regeneration plans (Chapman and Russo 2007). Though generalisations can be useful for this, there are always exceptions and as such they are no substitute for knowledge of local dispersal patterns (McConkey et al. 2012).

In tropical forests as many as 75% of trees and shrubs produce fleshy fruit suited for animal dispersal, with animals moving an estimated 95% of seeds (Chapman and Russo 2007). As seed dispersers, vertebrate frugivores play an important role in the regeneration of tropical forest habitats (Jansen and Zuidema 2001). Certain vertebrate groups may be of particular importance, for example primates which comprise 25 to 40% of frugivore biomass in tropical forests (Chapman 1995). Primates have been shown to disperse large numbers, of often viable, seed via defecation and spitting (Lambert 1998). Understanding the role they play in conservation and restoration projects is highly valuable, and may help inform a potentially cost effective approach to conservation efforts (Pullin and Knight 2003, Chapman and Russo 2007).

Animal mediated seed dispersal

Animal mediated seed dispersal is arguably the most important plant animal mutualism (Wunderle Jr 1997, Bowler and Benton 2005, Bascompte and Jordano 2007). Defined as transport of seeds away from the parent plant, seed dispersal is an important step in the reproductive cycle of most plants as it determines both the spatial arrangement and physical environment of seed distribution (Wenny 2000, Herrera 2002). Animal seed dispersal can benefit plants on an individual, population and community level (Augspurger 1984). Three main non-mutually exclusive, hypotheses are used to explain the benefits to plants at the individual and population level, these are:

1) Janzen-Connell/Escape hypothesis
2) Colonisation hypothesis
3) Directed dispersal

Escape hypothesis

Undispersed seeds typically fall beneath the parent tree (Nathan and Casagrandi 2004). This is especially true of those adapted to biotic dispersal (Howe and Smallwood 1982). A number have studies have shown that for many species

the probability of survival is lower under the parent due to density or distance dependent mortality (Augspurger 1984, Wilson and Traveset 2000, Herrera 2002). Under the escape hypothesis, seeds dispersed away from under the parents crown have a higher probability of survival as they escape from high levels of mortality due to increased numbers of host specific pathogens and seed predators associated with the parent, as well as from higher intraspecific competition (Augspurger 1984, Harms et al. 2000, Wang and Smith 2002).

Colonisation hypothesis

The colonisation hypothesis proposes that dispersal benefits plants as it provides the opportunity to colonise new habitats in which they have a competitive advantage (Augspurger 1984, Cain et al. 2000, Webb and Peart 2000, Babweteera and Brown 2010). Dispersal over a greater distance is associated with a higher probability of seed survival due to the increased likelihood that a seed will reach a light gap or other suitable habitat (Augspurger 1984). This is especially relevant in habitats when suitable sites for establishment are unpredictable or randomly distributed. This includes tropical forests where nearly all species need at least a small canopy gap to reach maturity and thus rely on stochastic events such as tree falls (Andresen 1999, Dupuy and Chazdon 2008).

Directed dispersal

Directed dispersal benefits plants via dispersal to sites favourable for germination and establishment (Wenny 2000). This ensures that a large proportion of seeds end up in favourable microhabitats, thereby increasing plant fitness. This requires that a disperser which preferentially carries seeds directly to sites that facilitate establishment at a rate higher than would result from chance (Wenny 2000, Howe and Miriti 2004).

Irrespective of which hypothesis or hypotheses are operating, animal mediated seed dispersal contributes significantly to the maintenance of plant population dynamics and community structure (Harms et al. 2000, Terborgh et al. 2002, Howe and Miriti 2004). In tropical forest as many as 90% of woody plants are dispersed by animals (Terborgh et al. 2002). These plant interact with an array of dispersers including birds, bats, as well as terrestrial and arboreal primates (Bleher and Böhning-Gaese 2001, Clark et al. 2001, Terborgh et al. 2002). These groups are highly diverse and it is unlikely that they disperse seed in comparable ways. Thus understanding the ecological forces that produce and maintain diversity requires detailed information on individual dispersers (Harms et al. 2000, Howe and Miriti 2004).

Primates constitute between 25 to 40% of the frugivore biomass in tropical forest (Kaplin and Lambert 2002). Consequently they are responsible for a significant portion of fruit consumption and thus play a key role in determining if large portions of seeds get effectively dispersed (Chapman 1995, Chapman and Russo 2007). Seed dispersal effectiveness is made up of two parts; the quantity of seeds dispersed and the quality of seed dispersal (Kaplin and Lambert 2002). Effective dispersal by primates depends on a number of key factors:

1) Number of seeds moved
2) How the seeds are handled
3) Whether seeds are dispersed to a location suitable for growth and avoidance of seed predation (Gross-Camp and Kaplin 2005).

These factors can vary between and within species depending on time of year, habitat and fruit abundance (Chapman and Russo 2007).

Effectiveness of seed dispersal

Plant species' recruitment, distribution and thus regeneration are heavily influenced by the effectiveness of their seed dispersers (Willson and Traveset 2000). Schupp (1993) stated seed dispersal effectiveness was best measured as the 'number of new adults produced by the dispersal activities of a disperser' and provided a framework within which it could be considered as the product of the quantity and quality of dispersal. Both of which are in turn determined by sub-components.

Quantity

Quantity is comprised of two sub-components:

1) The number of visits a disperser makes
2) The number of seeds dispersed per visit (Schupp et al. 2010)

For animal dispersed plants, successful dispersal requires movement of large numbers of seeds. This is due to the low probability of an individual seed produced by a tree successfully germinating and the even lower probability it will survive to maturity (Howe and Smallwood 1982). In turn both these sub-components are influenced by a number of variables. For the number of visits by a disperser species these include local abundance and the amount of fruit in their diet (Schupp et al. 2010). In turn, for the number of seeds dispersed per visit variables include how the fruit is handled by the frugivore, the number handled, and the body size of the disperser (Schupp et al. 2010). If disperser effectiveness is considered in terms of a forest, the number of different plant species fruits a disperser consumes is also important (Levin et al. 2003). From the perspective of the forest an effective disperser will consume a large variety of species, and large number of seeds from each species.

Quality

As with quantity, quality has two sub-components, each in turn influenced by a series of variables. These sub-components are:

1) Quality of treatment in mouth and gut
2) Quality of seed deposition (Schupp et al. 2010)

Quality of mouth and gut passage can alter seed dispersal effectiveness adversely via seed breakage and digestion, or have a positive or negative impact via altered germinability (Traveset 1998). Quality of seed deposition site has three demographic components:

1) Seed survival
2) Seedling emergence
3) Subsequent growth and survival (Schupp et al. 2010)

These in turn are impacted by a series of variables, these include herbivory, pathogens, germination requirements (light, fire etc.), competition and physiological requirements (Schupp et al. 2010).

To be effective seed handling by frugivores needs to increase seed viability (Willson and Traveset 2000). Frugivores that decrease viability via handling are considered seed predators, however the distinction for many species is not clear cut, with many species that act as dispersers also predating on seeds and vice versa (Schupp 1993). Even a highly effective disperser, will through handling, inevitably damage a few seeds amongst the many viable seeds it passes or spits. Conversely, even animals that are primarily seed predators can disperse a small number of viable seeds. Such an animal may have a disproportionate affect upon seedling recruitment if it disperses seeds into highly favourable microsites (Schupp 1993).

Seed viability can be positively, negatively or neutrally effected by primate gut passage, with positive effects occurring most frequently (Schupp 1993). Positive effects due to gut passage include increased germination rates and shortened latency time (Traveset 1998). They occur via the removal of pulp with germination inhibiting properties, scarification of seed coat, and/or co-deposition with faecal matter (Howe and Smallwood 1982). Negative effects occur when gut passage damages the seed to such a point that it is unable to germinate, including when the seed is destroyed due to digestive processes (Howe and Smallwood 1982).

Similarly, seed viability can be positively, negatively or neutrally effected by spitting of seeds by Cercopithecine monkeys (Kaplin and Lambert 2002). As with gut passage spitting may damage seeds, causing them to no longer be viable (Kaplin and Lambert 2002). It may also lower dispersal effectiveness as it tends to occur in closer proximity to the parent tree making the seed more susceptible to Janzen-Connell type effects (Chapman and Russo 2007). Positive effects have been proposed to occur due to the removal of pulp and cleaning of the seed (Lambert 2001). This may be beneficial as it may free the seed from inhibitory substances in the pulp, pulp removal may provide protection against seed predators, and anti-fungal protection (Lambert 2001).

Safe handling and movement away from the parent tree do not however guarantee that a seed will germinate and establish (Schupp et al. 2010). The physical environment of where the seed is deposited, and likelihood of encountering seed predators and secondary dispersers also have a significant impact (Nathan and Muller-Landau 2000). Suitability of a microsite is not static and exists on a continuum in both space and time. Furthermore, the suitability requirements of a site for germination is not necessarily the same as those for growth and survival (Wenny 2001). This means that generalisations on disperser quality and thus effectiveness may not hold true, with effectiveness varying with conditions in specific forests.

The overall effectiveness of a primate seed disperser depends on how well it meets a suite of requirements for successful dispersal (Schupp 1993). This will vary among species due to behavioural, physiological and morphological differences. Understanding a species dispersal effectiveness requires knowledge on both the quantity and quality of dispersal (Schupp et al. 2010). At the level of a forest this is not just an interaction with one fruit species but the quantity and quality of dispersal for the range of species in the frugivores diet (Levin et al. 2003). For species such as primates which have highly flexible diets, dispersal effectiveness and the species position on the disperser to predator

continuum may vary across time in response to availability. Therefore, studies of diet that focus on just one or two years, certain troops, or only certain age or sex classes may fail to capture the full breadth of a species diet and thus of its effectiveness as a seed disperser (Schupp 1993). Consumption of rare species may be missed if they are not available during the study period, or use of preferred foods missed is the study troop is being outcompeted and restricted to less favourable habitat. As a result decisions and management plans based on short studies may not have the anticipated benefit to forest restoration (Marshall and Wrangham 2007).

Guenons

The term Guenon lacks a clear historical root and can be used to refer to only monkeys in the genus *Cercopithecus* or more broadly to the group of closely related species and genera within the tribe Cercopithecini (Butynski 2002b). This is complicated by disagreement as to which species should be placed in *Cercopithecus,* and questions as to the validity of the genera *Miopithecus*, *Allenopithecus* and *Erythrocebus* within the Cercopithecini (Butynski 2002b). For the purposes of this thesis it will be used to refer to only members of the genus *Cercopithecus*. The number of species considered to be in this genera can vary considerably, ranging from 23 to 36 species, I will follow Moulin et al's (2008) definition which includes 26 species.

Guenons are a large and diverse group of small to medium sized monkeys found in sub-Saharan Africa. (Moulin et al. 2008). They have recently been identified as potentially important species in degraded habitats and are candidates for filling 'surrogate disperser' roles in African habitats (Albert et al. 2014). Most guenons are omnivorous, with diets consisting mainly of fruit, arthropods and leaves (Lambert et al. 2004). Other less common food items include pith, grass, gum, flowers, roots, mushrooms, fish, crabs, shrimp, eggs and small vertebrates (Butynski 2002a). Diets are highly flexible and can change between month, seasons, forests, troop, and different age and sex classes (Lambert 2002). Notably Gautier-Hion (1988a) found greater intra-specific variation in diet than inter-specific variation in sympatrically living guenons. This dietary flexibility is indicative of guenons characteristic ecological flexibility (Albert et al. 2014). Many guenons are robust to ecological disturbance, due to their ability to alter diet, group size, home range size and feeding methods in response to food availability and habitat structure (Lambert 2002). However their disturbance tolerance has led many to consider guenons pests (Albert et al. 2014). Subsequently many guenons roles as seed dispersers are still largely under studied (Kaplin and Lambert 2002, Hill and Webber 2010).

Almost all guenons live in groups comprising of a single male, multiple adult females, and their dependent offspring (Butynski 2002b). Though, during certain breeding seasons there may be a temporary influx of additional males (Henzi and Lawes 1988, Struhsaker 1988, Cords 2000). The exception to this is *C. neglectus* (DeBrazza's monkey) which may also live in family groups consisting of one adult male and only one adult female (Butynski 2002b). Guenons exhibit sexual dimorphism in weight with males on average weighing around 5.9 kg and females 3.6 kg (Butynski 2002b). The majority of guenons have distinct mating and birth seasons, which tend to coincide with variations in food availability and rainfall (Butynski 2002a). One species, *C. Ascanius* (red-tailed monkey), is known to give birth all year round. However, 97% of births occur during a birth peak from April to November (Cords 1984).

Ranging behaviour varies among guenons, most likely in response to varying resource abundance and distribution between habitats (Enstam and Isbell 2002). Home range size varies from as little as 4 ha in *C. neglectus,* up to 335 ha in *C. mitis* (blue monkey) and day range length from 530m in *C. neglectus* to 2,092 in *C. ihoesti* (l'Hoest's monkey) (Enstam and Isbell 2002). Guenons live in a range of forest habitats including primary, secondary and gallery rain forest, bamboo forest, and flooded and swamp forest. Just over 72% of guenon species are tolerant to living in secondary forest and of these around 28% are able to persist in heavily disturbed areas, such as pasture, plantation and rural gardens (Albert et al. 2014). Guenons are often found living in sympatry with other guenon species, and they are known to form communities with other guenons, mangabeys and colobines. These polyspecific associations can range from transient to nearly permanent (Gautier-Hion 1988b, Enstam and Isbell 2007). Both this ability to live in sympatry and tolerance to disturbance is believed to be due to guenons' aforementioned ecological flexibility.

These polyspecific associations have also been proposed to have played a role in the evolution of the striking diversity of facial patterns observed in guenons. Kingdon (2007) noted that despite being very similar in gross anatomy (medium sized, long back legs, rounded head, long tail and large check pouches) and behaviour, guenons had strikingly distinct facial patterns he termed 'flags'. In the Cercopithecini tribe, the broader definition of guenon, it has been found that these have undergone character displacement (Allen et al. 2014). Having evolved under selection to be most dissimilar from other Cercopithecini with whom they are sympatric. These patterns act as pre-zygotic reproductive isolating barriers and though instances of hybridisation have occurred in captivity they are relatively rare in the wild. Facial patterns role as an isolating barrier is further supported by head flagging behaviours observed in guenons, where species move their head in characteristic patterns to enhance the facial markings in sexual and aggressive signalling behaviours (Kingdon 1980, Allen et al. 2014).

Cercopithecinae, including guenons, are unique amongst primates in that they can disperse seeds in three ways:

1) Epizoochory (dispersal via the outside of the animal – dropping)
2) Endozoochroy (dispersal by swallowing and defecation) and
3) Synzoochory (dispersal by storing in cheek pouches and spitting) (Yumoto et al. 1998).

The same species will vary seed handling techniques according to plant species, phenology patterns, and resource availability (Kaplin et al. 1998, Tsujino and Yumoto 2009). This may increase seed survival as it creates a unique seed shadow, with spat seeds closer to the parent tree and potentially less clumped than defecated seeds (Stoner et al. 2007, Schupp et al. 2010, McConkey and Brockelman 2011).

Traditionally seed spitting was considered an ineffective mode of dispersal, with around 80% of seed deposited under the parent's crown (Lambert and Garber 1998, Albert et al. 2014). More recently spitting has been identified to have a number of potential benefits. It may allow Cercopithecinae to disperse larger seeds than what they would swallow (Gross-Camp and Kaplin 2011), and to potentially consume more fruit. Increased consumption is possible as the monkey is not bulked down with inert seed mass in their gut (Corlett and Lucas 1990, McConkey and Brockelman 2011). Furthermore, as cheek pouches can have nearly the same capacity as the monkey's stomach, a large number of seeds can be distributed (Chapman and Russo 2007). It has also been proposed that spitting seeds may increase

dispersal efficiency compared to defecation by increasing seedling establishment (Albert et al. 2014). This may be due to the removal of the pulp removing a scent cue for seed predators, providing protection from fungal pathogens or releasing the seed from inhibitory chemicals found in the flesh. Though studies have found support for this hypothesis in a few species (Lambert 2001, Balcomb and Chapman 2003, Gross-Camp and Kaplin 2011), Chapman et al. (2010) found mixed effects for *C. nictitans* (putty-nosed monkeys). They found that spitting had non-significant effects on two species (*Deinbollia pinnata* and *Isolona* cf. *deightonii*) and a detrimental effect on a third (*Santiria trimera*). This is likely reflective of the differential importance of dispersal and factors in different plant species and highlights the need for further research on guenon seed dispersal.

Amongst guenons, it has been previously proposed that *C. nictitans* may be a potentially important seed disperser in disturbed Afromontane forest, due to its potential capacity to disperse medium to large seeds which may allow it to compensate for the loss of other large bodied seed dispersers (Chapman et al. 2010).

Cercopithecus nictitans

Cercopithecus nictitans is a guenon in the *C. nictitans* group, and is native to Central West Africa (Butynski 2002a). Its distribution is disjunct with populations in Liberia and western Côte d'Ivoire and on the island of Bioko (Equatorial Guinea), and a more continuous population from western Nigeria, south and east to the Congo River and across the Oubangui River through to Buta and Budjala in the Democratic Republic of the Congo (Oates and Groves 2008). Primarily arboreal, it is commonly found in lowland and montane tropical moist forest, gallery forest, secondary forest, and less commonly in swamp forest (Bitty and McGraw 2007).

Cercopithecus nictitans is commonly known as the greater spot-nosed monkey or putty nosed monkey, due to the prominent white spot over its nose (Oates and Groves 2008). Elsewhere, *C. nictitans* has a mostly drab olive green, grey or black colouration causing the white spot to prominently stand out (Kingdon 1988). Individuals may also have a white patch on the chest and/or red brown patches on their foreheads and base of tail. These variations in colouration have been attributed to various sub-species (Oates and Nash 2011). Body size ranges from 43 to 70 cm, with a long tail between 56 and 100 cm long (Butynski 2002a). Body weight is between 4.2 and 6.6 kg, with sexual dimorphism evident in both greater body weight and body length in males (Oates and Groves 2008). Dentition is similar to *C. diana* and resource competition between species is believed to contribute to the isolated western range (Oates and Groves 2008).

Troop size typically ranges from 12 to 30 individuals, with troops of up to 60 having been reported (Tutin 1999, Chapman et al. 2002, Eckardt and Zuberbühler 2004, Arnold and Zuberbühler 2008, Oates and Groves 2008). Troops consist of a single adult male, multiple adult females and their dependent offspring with male tenures of five years common (Cords 1987, Estes 1991). Both troops and solo-males form polyspecific associations with other monkey species, which can be transient to semi-permanent (Stensland et al. 2003, Eckardt and Zuberbühler 2004). Hybrids as a consequence of these associations have been known to occur in both captivity and in the wild (Tutin 1999).

There is little information available on the reproductive cycle, breeding season, and parental investment. Females mature around four years of age and give birth approximately every two years (De Magalhaes and Costa 2009). It has

been assumed that similar to other guenons young will be relatively well developed at birth and remain with their mothers for approximately six months (De Magalhaes and Costa 2009). In captivity individuals have been known to live up to 31 years old, with life span in the wild approximated at 21 years (De Magalhaes and Costa 2009).

Cercopithecus nictitans have primarily been identified as frugivorous and granivorous (Fa and Purvis 1997). However work to date has only been conducted in six study sites, with all studies bar one being conducted in lowland continuous forest (Gautier-Hion 1980, Gautier-Hion 1988a, Mitani 1991, Tutin et al. 1997, Tutin and White 1998, Brugiere et al. 2002, Poulsen et al. 2002). The exception was conducted in a lowland fragment, in the same reserve as an earlier study (Tutin et al. 1997, Tutin 1999). This tendency toward seed consumption has led to *C. nictitans*, like many other guenons, to be considered a seed predator (Albert et al. 2014). Recent research however indicates that this may not always be so. Work in a Nigerian montane forest found a notable amount of viable seed in faecal deposits (Chapman et al. 2010). This included species they identified as medium (>5mm) and large (≥15mm) seeded and which due to a loss of large bodied dispersers in the reserve may be at risk of dispersal crisis (Chapman et al. 2010). It may be that the focus on lowland continuous forest has resulted in this potentially important role of *C. nictitans* as a seed disperser in montane and/or disturbed forests.

The potential for *C. nictitans* to disperse at risk seed species, along with studies showing potential benefits in seed spitting in guenons, indicates that contrary to previous thought they may be effective seed dispersers. This may be especially true in disturbed and fragmented forests, a habitat in which they have been little studied, due to both their potential ecological flexibility and the high extinction risk to other large bodied dispersers in these environments. It is therefore important to determine *C. nictitans* diets in different habitats and how diet responds to scarcity to determine their full potential to act as effective seed dispersers in disturbed and fragmented forests.

Nigerian Afromontane forests

Occuring along the Cameroon Volcanic line at elevations above 1,500 m, Nigerian montane forests are considered bio-diversity hot spots (Myers et al. 2000). Of the rare tropical dry forest type (have annual hard dry seasons) they continue to harbour many threatened plant and animal species despite dramatic reductions in wildlife (Chapman et al. 2004).

Montane forests are particularly vulnerable to anthropogenic habitat fragmentation and climate change (Pounds et al. 1999, Inouye 2008). By recent measures Nigeria has the second highest rate of deforestation in the world, with a 55.7% decrease in primary forest between 2000 and 2005 (Blaser 2011). An increase in human populations and related agricultural practices (burning and grazing by cattle) has caused Nigerian Afromontane regions to be particularly vulnerable to extinction (Chapman et al. 2004).

Enforcement of conservation policies and forest regeneration are two alternatives to try and mitigate the effects of habitat loss, however both contain intrinsic challenges (Blaser 2011). Most notably the high cost of patrolling, monitoring and replanting operations (Chapman and Chapman 1995, Vieira and Scariot 2006). It has therefore been

suggested that the most cost effective method would be to utilise the existing plant animal mutualisms (Chapman and Chapman 1995, McConkey et al. 2012).

Field Site

The study was conducted at Ngel Nyaki Forest Reserve, a submontane forest reserve located on the western escarpment of Mambilla Plateau (7°30 N, 11°30 E), in Taraba State, Nigeria at elevations between 1400-1600 MAMSL (Fig 1). Ngel Nyaki is a moderately-large forest approximately 5.3 km^2, surrounded by a number of smaller riparian fragments (Chapman and Chapman 2001). Mean monthly minimum and maximum temperatures for the wet and dry seasons are 26 and 13°C, and 23 and 16°C respectively. Mean annual rainfall is approximately 1,800mm, occurring predominantly between April and October (Nigerian Montane Forest Project Weather data).

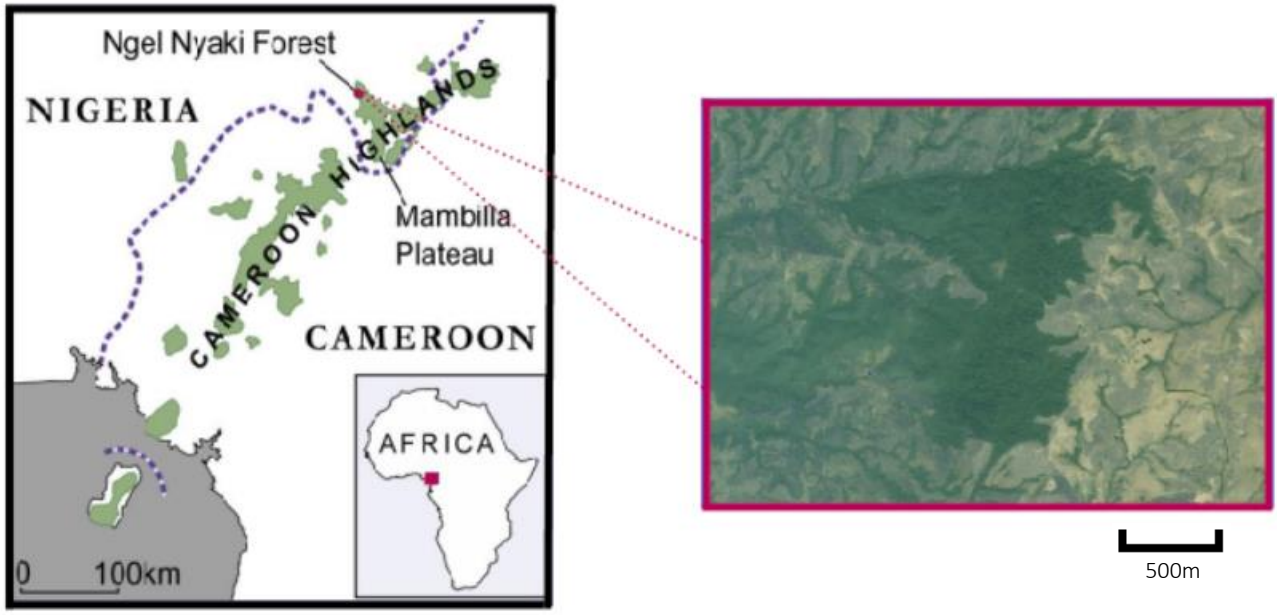

Fig 1. A map of the Cameroon Highlands. Illustrating the location of Ngel Nyaki Forest Reserve, Nigeria, where this study was conducted. SOURCE: modified from Beck and Chapman (2008). **Insert:** Satellite image showing Ngel Nyaki forest, nearby Kurmin Danko forest and surrounding riparian fragments. Source: modified from map data ©2015 Google

Ngel Nyaki Forest Reserve is one of the most floristically diverse forests in Nigeria, containing many endemic plant species, including several on the IUCN red list (Chapman et al. 2004). Despite facing pressures from slash and burn agriculture, cattle trampling and hunting, the forest is still relatively abundant in wildlife (Chapman et al.2004). In addition to *C. nictitans* it is home to five other primate species, the critically endangered *Pan troglodytes ellioti,* locally rare *Papio anubis, Cercopithecus mona* and *Colobus guereza occidentalis,* and the locally common *Chlorocebus tantalus tantalus* (Chapman et al. 2004).

Current conservation efforts at Ngel Nyaki Forest include the controlled 'early burning' of fire breaks around the forest to prevent fires encroaching into the forest, the fencing off areas of grassland to prevent cattle grazing to allow forest

regeneration, and replanting (Beck and Chapman 2008). Additionally, the forest is regularly patrolled to deter hunters (NMFP Annual Report)

Given the increasing evidence that *Cercopithecus* sp. may be an important seed disperser, and in particular that *C. nictitans* may be a compensatory disperser of medium to large seeds in disturbed Nigerian montane forests, it is important we gain a better understanding of their diet. This includes how and when it may vary in result to stressors such as a decrease in food availability. To help better understand this I compared the diet of *C. nictitans* living in Ngel Nyaki Forest over three years with the goal of gaining insight in to its role as a potential seed dispersers and how this alters with food availability, fruit characteristics, troop size and sex.

References

Achard, F., R. Beuchle, P. Mayaux, H. J. Stibig, C. Bodart, A. Brink, S. Carboni, B. Desclée, F. Donnay, and H. D. Eva. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. Global change biology **20**:2540-2554.

Albert, A., K. McConkey, T. Savini, and M.-C. Huynen. 2014. The value of disturbance-tolerant cercopithecine monkeys as seed dispersers in degraded habitats. Biological Conservation **170**:300-310.

Allen, W. L., M. Stevens, and J. P. Higham. 2014. Character displacement of Cercopithecini primate visual signals. Nature communications **5**:DOI: 10.1038/ncomms5266.

Andresen, E. 1999. Seed Dispersal by Monkeys and the Fate of Dispersed Seeds in a Peruvian Rain Forest1. Biotropica **31**:145-158.

Arnold, K., and K. Zuberbühler. 2008. Meaningful call combinations in a non-human primate. Current Biology **18**:doi:10.1016/j.cub.2008.1001.1040.

Asongu, S. A., and B. A. Jingwa. 2012. Population growth and forest sustainability in Africa. International Journal of Green Economics **6**:145-166.

Augspurger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology **65**:1705-1712.

Babweteera, F., and N. Brown. 2010. Spatial patterns of tree recruitment in East African tropical forests that have lost their vertebrate seed dispersers. Journal of Tropical Ecology **26**:193-203.

Balcomb, S. R., and C. A. Chapman. 2003. Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecological Monographs **73**:625-642.

Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. Annual review of ecology, evolution, and systematics **38**:567-593.

Bitty, E. A., and W. S. McGraw. 2007. Locomotion and habitat use of Stampflii's putty-nosed monkey (*Cercopithecus nictitans stampflii*) in the Taï National Park, Ivory Coast. American Journal of Physical Anthropology **134**:383-391.

Blaser, J. 2011. Status of tropical forest management 2011. International Tropical Timber Organization.

Bleher, B., and K. Böhning-Gaese. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. Oecologia **129**:385-394.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews **80**:205-225.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, and G. Magin. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation biology **16**:909-923.

Brugiere, D., J.-P. Gautier, A. Moungazi, and A. Gautier-Hion. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology **23**:999-1024.

Butynski, T. M. 2002a. The guenons: An overview of diversity and taxonomy. Pages 3-13 The guenons: Diversity and adaptation in African monkeys. Springer.

Butynski, T. M. 2002b. The guenons: Diversity and adaptation in African monkeys. Kluwer Academic, New York.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany **87**:1217-1227.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Chapman, C. A. 1995. Primate seed dispersal: coevolution and conservation implications. Evolutionary Anthropology: Issues, News, and Reviews **4**:74-82.

Chapman, C. A., and L. J. Chapman. 1995. Survival without dispersers: seedling recruitment under parents. Conservation biology **9**:675-678.

Chapman, C. A., L. J. Chapman, M. Cords, J. M. Gathua, A. Gautier-Hion, J. E. Lambert, K. Rode, C. E. Tutin, and L. J. White. 2002. Variation in the diets of Cercopithecus species: differences within forests, among forests, and across species. Pages 325-350 The guenons: Diversity and adaptation in African monkeys. Springer.

Chapman, C. A., and J. E. Lambert. 2000. Habitat Alteration and the Conservation of African Primates: Case Study of Kibale National Park, Uganda. American journal of primatology 50:169-185.
Chapman, C. A., and D. A. Onderdonk. 1998. Forests without primates: primate/plant codependency. American journal of primatology 45:127-141.
Chapman, C. A., and C. A. Peres. 2001. Primate conservation in the new millennium: the role of scientists. Evolutionary anthropology 10:16-33.
Chapman, C. A., and S. E. Russo. 2007. Primate seed dispersal. Primates in perspective. New York: Oxford University Press:510-525.
Chapman, H. M., S. L. Goldson, and J. Beck. 2010. Postdispersal removal and germination of seed dispersed by Cercopithecus nictitans in a West African montane forest. Folia Primatologica 81:41-50.
Chapman, H. M., S. M. Olson, and D. Trumm. 2004. An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. Oryx 38:282-290.
Chapman, J., and H. Chapman. 2001. The Forests of Taraba and Adamawa States, Nigeria. *An Ecological Account and Plant Species Checklist*. University of Canterbury, New Zealand.
Clark, C., J. Poulsen, and V. Parker. 2001. The Role of Arboreal Seed Dispersal Groups on the Seed Rain of a Lowland Tropical Forest1. Biotropica 33:606-620.
Cords, M. 1984. Mating patterns and social structure in redtail monkeys (Cercopithecus ascanius). Zeitschrift für Tierpsychologie 64:313-329.
Cords, M. 1987. Mixed-species association of Cercopithecus monkeys in the Kakamega Forest, Kenya, by Marina Cords. University of California Publications in Zoology 117.
Cords, M. 2000. The number of males in guenon groups. Primate males: Causes and consequences of variation in group composition:84.
Corlett, R., and P. Lucas. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). Oecologia 82:166-171.
Cramer, J. M., R. C. Mesquita, and G. B. Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation 137:415-423.
De Magalhaes, J., and J. Costa. 2009. A database of vertebrate longevity records and their relation to other life-history traits. Journal of evolutionary biology 22:1770-1774.
DeFries, R. S., T. Rudel, M. Uriarte, and M. Hansen. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. Nature Geoscience 3:178-181.
Dupuy, J. M., and R. L. Chazdon. 2008. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. Forest Ecology and Management 255:3716-3725.
Eckardt, W., and K. Zuberbühler. 2004. Cooperation and competition in two forest monkeys. Behavioral Ecology 15:400-411.
Enstam, K. L., and L. A. Isbell. 2002. The Guenons (Genus *Cercopithecus*) and Their Ailies.*in* C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder, editors. Primates in perspective. Oxford University Press, Oxford, UK.
Enstam, K. L., and L. A. Isbell. 2007. The guenons (genus Cercopithecus) and their allies: behavioral ecology of polyspecific associations. Primates in perspective:252-274.
Estes, R. 1991. The behavior guide to African mammals. University of California Press Berkeley, California.
Fa, J. E., and A. Purvis. 1997. Body size, diet and population density in Afrotropical forest mammals: a comparison with neotropical species. Journal of animal ecology 66:98-112.
Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics 34:487-515.
Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. The Journal of Animal Ecology 49:237-269.
Gautier-Hion, A. 1988a. The diet and dietary habits of forest guenons. Pages 257-283 A primate radiation: Evolutionary biology of the African guenons. Cambridge University Press, Cambridge.
Gautier-Hion, A. 1988b. Polyspecific associations among forest guenons: ecological, behavioural and evolutionary aspects. Pages 452-476 A primate radiation: Evolutionary biology of the African guenons. Cambridge University Press, Cambridge.
Gross-Camp, N. D., and B. A. Kaplin. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. Acta Oecologica 37:578-586.

Gross-Camp, N., and B. A. Kaplin. 2005. Chimpanzee (*Pan troglodytes*) Seed Dispersal in an Afromontane Forest: Microhabitat Influences on the Postdispersal Fate of Large Seeds. Biotropica **37**:641-649.
Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. Turubanova, A. Tyukavina, D. Thau, S. Stehman, S. Goetz, and T. Loveland. 2013. High-resolution global maps of 21st-century forest cover change. Science **342**:850-853.
Hanski, I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio **40**:248-255.
Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404**:493-495.
Henzi, S., and M. Lawes. 1988. Strategic responses of male samango monkeys (Cercopithecus mitis) to a decline in the number of receptive females. International Journal of Primatology **9**:479-495.
Herrera, C. M. 2002. Seed dispersal by vertebrates. Plant-animal interactions: an evolutionary approach **185**:208.
Hill, C. M., and A. D. Webber. 2010. Perceptions of nonhuman primates in human–wildlife conflict scenarios. American journal of primatology **72**:919-924.
Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. BioScience **54**:651-660.
Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual review of ecology and systematics **13**:201-228.
Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology **89**:353-362.
Isabirye-Basuta, G. M., and J. S. Lwanga. 2008. Primate populations and their interactions with changing habitats. International Journal of Primatology **29**:35-48.
Jansen, P. A., and P. A. Zuidema. 2001. Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees. Pages 35-60 The cutting edge: conserving wildlife in logged tropical forests. . Columbia University Press, New York.
Jha, S., and K. S. Bawa. 2006. Population growth, human development, and deforestation in biodiversity hotspots. Conservation biology **20**:906-912.
Kaplin, B., V. Munyaligoga, and T. Moermond. 1998. The Influence of Temporal Changes in Fruit Availability on Diet Composition and Seed Handling in Blue Monkeys (*Cercopithecus mitis doggetti*). Biotropica **30**:56-71.
Kaplin, B. A., and J. E. Lambert. 2002. Effectiveness of Seed Dispersal by Cercopithecus Monkeys: Implications for Seed Input into Degraded Areas.*in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, New York.
Kingdon, J. 1980. The role of visual signals and face patterns in African forest monkeys (guenons) of the genus Cercopithecus. The Transactions of the Zoological Society of London **35**:425-475.
Kingdon, J. 1988. What are face patterns and do they contribute to reproductive isolation in guenons. Pages 227-245 A primate radiation: Evolutionary biology of the African guenons. Cambridge University Press, Cambridge, UK.
Kingdon, J. 2007. Primate visual signals in noisy environments. Folia Primatologica **78**:389-404.
Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, and J. Pino. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology letters **13**:597-605.
Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. Science **310**:1628-1632.
Lambert, J. E. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology: Issues, News, and Reviews **7**:8-20.
Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and Strychnos mitis: evidence for plant benefits beyond seed dispersal. International Journal of Primatology **22**:189-201.
Lambert, J. E. 2002. Resource switching and species coexistence in guenons: A community analysis of dietary flexibility. Pages 309-323 The Guenons: Diversity and adaptation in African monkeys. Springer, New York.
Lambert, J. E., C. A. Chapman, R. W. Wrangham, and N. L. Conklin-Brittain. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. American Journal of Physical Anthropology **125**:363-368.
Lambert, J. E., and P. A. Garber. 1998. Evolutionary and ecological implications of primate seed dispersal. American journal of primatology **45**:9-28.
Laurance, W. F., D. C. Useche, J. Rendeiro, M. Kalka, C. J. Bradshaw, S. P. Sloan, S. G. Laurance, M. Campbell, K. Abernethy, and P. Alvarez. 2012. Averting biodiversity collapse in tropical forest protected areas. Nature **489**:290-294.
Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual review of ecology, evolution, and systematics **34**:575-604.

Linard, C., M. Gilbert, R. W. Snow, A. M. Noor, and A. J. Tatem. 2012. Population distribution, settlement patterns and accessibility across Africa in 2010. PloS one **7**:DOI: 10.1371/journal.pone.0031743.
Marsh, L. K., and B. A. Loiselle. 2003. Recruitment of black howler fruit trees in fragmented forests of Northern Belize. International Journal of Primatology **24**:65-86.
Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology **28**:1219-1235.
McConkey, K. R., and W. Y. Brockelman. 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology **92**:1492-1502.
McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biological Conservation **146**:1-13.
Mitani, M. 1991. Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. Primates **32**:137-151.
Moran, C., C. Catterall, R. J. Green, and M. F. Olsen. 2004. Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. Oecologia **141**:584-595.
Moulin, S., M. Gerbault-Seureau, B. Dutrillaux, and F. A. Richard. 2008. Phylogenomics of African guenons. Chromosome Research **16**:783-799.
Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.
Nathan, R., and R. Casagrandi. 2004. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. Journal of Ecology **92**:733-746.
Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in ecology & evolution **15**:278-285.
Nepstad, D., B. S. Soares-Filho, F. Merry, A. Lima, P. Moutinho, J. Carter, M. Bowman, A. Cattaneo, H. Rodrigues, and S. Schwartzman. 2009. The end of deforestation in the Brazilian Amazon. Science **326**:1350-1351.
Oates, J. F., and C. P. Groves. 2008. *Cercopithecus nictitans*.
Oates, J. F., and S. D. Nash. 2011. Primates of West Africa: a field guide and natural history. Conservation International Arlington, Virginia.
Pimm, S. L., and P. Raven. 2000. Biodiversity: extinction by numbers. Nature **403**:843-845.
Poulsen, J. R., C. J. Clark, E. F. Connor, and T. B. Smith. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. Ecology **83**:228-240.
Pounds, J. A., M. P. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature **398**:611-615.
Pullin, A. S., and T. M. Knight. 2003. Support for decision making in conservation practice: an evidence-based approach. Journal for Nature Conservation **11**:83-90.
Ruxton, G. D., and H. M. Schaefer. 2012. The conservation physiology of seed dispersal. Philosophical Transactions of the Royal Society B: Biological Sciences **367**:1708-1718.
Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Pages 15-29 Frugivory and seed dispersal: ecological and evolutionary aspects. Springer, Netherlands.
Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist **188**:333-353.
Stensland, E., A. Angerbjörn, and P. Berggren. 2003. Mixed species groups in mammals. Mammal Review **33**:205-223.
Stoner, K. E., P. Riba-Hernández, K. Vulinec, and J. E. Lambert. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica **39**:316-327.
Struhsaker, T. 1988. Male tenure, multi-male influxes, and reproductive success in redtail monkeys (Cercopithecus ascanius). A primate radiation: Evolutionary biology of the African guenons:340-363.
Terborgh, J., G. Nuñez-Iturri, N. C. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. T. Paine. 2008. Tree recruitment in an empty forest. Ecology **89**:1757-1768.
Terborgh, J., N. Pitman, M. Silman, H. Schichter, and P. Núñez. 2002. Maintenance of tree diversity in tropical forests. Pages 1-17 Seed dispersal and frugivory: ecology, evolution and conservation. . CABI Publishing, Wallingford, UK.
Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Perspectives in Plant ecology, evolution and systematics **1**:151-190.
Tsujino, R., and T. Yumoto. 2009. Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. Journal of animal ecology **78**:119-125.

Tutin, C., R. Ham, and L. White. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American journal of primatology **42**:1-24.
Tutin, C., and L. White. 1998. Primates, phenology and frugivory: Present, Past and Future Patterns in the Lopé Reserve, Gabon. Page 309 *in* Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society. Cambridge University Press.
Tutin, C. E. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates **40**:249-265.
Vieira, D. L., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. Restoration Ecology **14**:11-20.
Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. Trends in ecology & evolution **17**:379-386.
Webb, C. O., and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. Journal of Ecology **88**:464-478.
Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecological Monographs **70**:331-351.
Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research **3**:37-50.
Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American naturalist **125**:879-887.
Willson, M. F., and A. Traveset. 2000. The ecology of seed dispersal. Seeds: The ecology of regeneration in plant communities **2**:85-110.
Wilson, M., and A. Traveset. 2000. The ecology of seed dispersal. In 'Seeds: The Ecology of Regeneration in Plant Communities'.(Ed. M. Fenner.) pp. 85–110. CABI Publishing: Wallingford, UK.
Wunderle Jr, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**:223-235.
Yumoto, T., N. Noma, and T. Maruhashi. 1998. Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates **39**:325-338.

2| Diet and response to scarcity of *C. nictitans* living in Ngel Nyaki Forest Reserve, Nigeria

Introduction

Habitat loss and fragmentation pose serious risks to biodiversity (Zuidema et al. 1996, Dirzo and Raven 2003, Fahrig 2003, Hanski 2005, Krauss et al. 2010). Loss of forest results in not only loss of their intrinsic value but also of the ecosystem services that they provide, including soil and water conservation, CO_2 sequestration, and provision of food and medicinal plants (Duncan and Chapman 2002, Fearnside 2005, Foley et al. 2005). Although tragic in their own right, extinctions of animal populations in tropical forests may have important repercussions for the entire forest ecosystem, perpetrated through changes to critical plant-animal interactions such as seed dispersal (Peres 2001; Stoner *et al*. 2007; Corlett 2007; Wright *et al*. 2007) and pollination (Biesmeijer 2006; Memmott *et al*. 2007). Such changes to species interactions can be more difficult to document and quantify than species extinctions per se, but they are of paramount importance for the stability and functioning of ecosystems (McCann 2007; Thomson 2006; Bascompte *et al*. 2006).

Nigeria has the second highest rate of deforestation in the world, losing on average, 4% of its forests per year between 2005 and 2010 (Blaser 2011). During this period the area of primary forest declined from 326,000 ha to effectively zero, with only small areas of intact forest remaining in rugged terrain (Food and Nations 2010). While State-Owned forest reserves account for around three-quarters of total forest area, in Nigeria, this does not mean they are necessarily protected; 60 % of the initial 3.92 million ha set aside as forest reserves in 1960s had been lost by 2010 (Blaser 2011). Despite policy changes in 2004, there is no real indication that the situation has changed and in the face of a rapidly increasing human population means that even these supposedly protected areas remain vulnerable to exploitation (Blaser 2011).

Habitat loss and fragmentation not only affect the plants that make up the forest, but also the wildlife species living in and around them (Chapman and Onderdonk 1998, Pimm and Raven 2000, Brooks et al. 2002, Fahrig 2003). Large bodied animal species in particular have a high extinction risk due to both intrinsic and environmental factors; they

tend to live at lower population densities, have a lower intrinsic rate of population increase, and tend to be subject to higher hunting pressure (Wilcox and Murphy 1985, Cardillo et al. 2005). However, despite being found at low densities, large bodied species can have a disproportionately large impact on their ecosystem. For example, Wrangham et al. (1994) found that despite comprising 1.4% of the primate frugivore population and 14.2% of primate frugivore biomass, *Pan troglodytes* (common chimpanzee) accounted for around 45.3% of seeds defecated by frugivorous primates. Moreover large bodied primates may also be the only taxa capable of dispersing large seeds and subsequently that particular plant species may be dependent on large frugivores to persist (Moran et al. 2004, Cramer et al. 2007, Ruxton and Schaefer 2012). The impact of this may be particularly drastic in tropical forest systems, where up to 90% of woody plants produce fleshy fruit adapted for animal dispersal. In such systems, loss of wildlife can lead to changes in fruit dispersal patterns and a subsequent change in community composition (Chapman et al. 2010, McConkey et al. 2012).

Habitat regeneration is necessary for both the conservation of biodiversity and the maintenance of the ecosystem processes (Parrotta et al. 1997, Sorensen and Fedigan 2000, Dirzo and Raven 2003, Moberg and Rönnbäck 2003). Wide-spread forest regeneration can however be cost prohibitive; Vieira and Scariot (2006) reported enriching a forest fragment in Brazil as cost as much as $1,050/ha (USD). The cost of regeneration can in part be mitigated if biological processes that perpetuate regeneration, such as primate seed dispersal, are encouraged as these come at little or no cost. To do so requires an understanding of the complex interplay of ecological processes that maintain forest diversity, including detailed information on individual dispersers (Wunderle Jr 1997, Duncan and Chapman 2002).

The ongoing loss of large bodied dispersers from a range habitats is placing current plant-disperser relationships at risk (Clout and Hay 1989, Cordeiro and Howe 2003, McConkey and Drake 2006, Albert et al. 2014). Reintroduction or targeted conservation of functionally extinct species may allow us to regain lost seed-disperser interactions (Polak et al 2014) however, this scenario is often impossible to the wide spread extirpation of large bodied frugivorous (Bond 1994). In such cases the use of other species as 'surrogate dispersers' may instead be considered, with the best candidates most likely to be local or regional fauna with appropriate functional roles (McConkey, Prasad et al. 2012). Once identified, 'surrogate disperser' species can be re-introduced or supported in situ via targeted conservation efforts (Albert et al. 2014). Identifying potential surrogate species requires knowledge of their diet and how diet

responds to causes of scarcity such as forest loss and fragmentation (Harms et al. 2000, Howe and Miriti 2004). . For example, a species that increases seed predation during times of scarcity would be an ill-suited candidate. Similarly, a surrogate disperser should be robust to disturbance or it too, risks being lost.

Cercopithecinae as a surrogate disperser

Cercopithecine monkeys have been identified as potentially important species in degraded habitats and are potential candidates for filling 'surrogate disperser' roles in Asian and African habitats (Albert et al. 2014). Characterised by possessing check pouches, Cercopithecinae are unique amongst primates in that they can disperse seeds in three ways; dropping, defecation and spitting (Yumoto et al. 1998). The same Cercopithecine species can vary seed processing techniques according to plant species, phenology patterns and resource availability (Kaplin et al. 1998, Tsujino and Yumoto 2009), creating a unique seed shadow, in turn increasing the probability a proportion of seed will be dispersed into suitable microhabitats (Stoner et al. 2007, Schupp et al. 2010, McConkey and Brockelman 2011). Furthermore, the unique spitting behaviour allows Cercopithecine to disperse larger seeds than their size as it spares the need for seeds to pass through the alimentary canal (Gross-Camp and Kaplin 2011).

Cercopithecinae is characterised by ecological flexibility with most species able to vary group size, diet, home range and feeding methods in response to resource availability and habitat structure (Stoner, Riba-Hernández et al. 2007). As a result nearly 80 % of species persist in disturbed habitat (Albert et al 2014). This means many species have potential as surrogate dispersers in disturbed habitats, where more specialised species can no longer persist (Albert et al. 2014). This disturbance tolerance however, has led many people to mostly consider Cercopithecinae as pests. This has resulted in their role as potentially important seed dispersers has been largely ignored until recently (Kaplin and Lambert 2002, Hill and Webber 2010).

Chapman et al. (2010) proposed that in Ngel Nyaki Forest Reserve (NMFP), an Afromontane forest in Nigeria, *Cercopithecus nictitans* (putty-nosed monkey) may be a 'surrogate disperser', partially offsetting the loss of the previously common *Pan troglodytes ellioti* (Nigerian/Cameroon chimpanzee). The severe reduction in *P. t. elotti* biomass and the extinction of *Loxodonta africana* (African forest elephant) means that large fruited species at NMFP may be undergoing a seed dispersal crisis, having effectively lost two of the small set of dispersers with large enough gapes to consume them (Borokini et al. 2012, Thia 2014).

Like many other *Cercopithecus* Spp., until recently *C. nictitans* was thought to be a seed predator (Happel 1988, Rowell and Mitchell 1991), and their potential role as seed disperser, including diet and feeding ecology has subsequently been understudied (Kaplin and Lambert 2002, Albert, McConkey et al. 2014). From Chapman et al.'s (2010) work however there are indications that *C. nictitans* may be able to compensate somewhat for larger frugivores; they can defecate seeds with a mean length of up to 24.7mm, comparable to findings in the same forest by Dutton and Chapman (2015) for *P. t. ellioti,* where the largest seed found in faecal matter had a mean length of 28.5mm. However, as little is known about the diet of *C. nictitans,* it is unclear whether this ability translates into substitute dispersal, or if instead, as has been presumed historically, they are seed predators.

Previous studies on *C. nictitans* diet

To the best of my knowledge, there have only been six published studies into the diet of *C. nictitans,* four of which were conducted in Gabon (Gautier-Hion 1980, Gautier-Hion 1988, Tutin et al. 1997, Tutin and White 1998, Tutin 1999, Brugiere et al. 2002), and two in Cameroon (Mitani 1991, Poulsen et al. 2002) (Table 1). Methodology and reporting across studies is inconsistent, restricting the confidence that may be placed in any direct comparison between sites. Moreover, *Cercopithecus* spp. behaviour and diet can vary between and even within forests (Chapman et al. 2002) in response to a number of variables including differences in polyspecific associations (Gautier-Hion et al. 1983), forest type (Gautier-Hion et al. 1981), disturbance (Tutin 1999) and food availability (Lawes 1991, Wrangham et al. 1998). The variability between most sites means that factors that influence variation are difficult to determine, and that it would be incorrect to try do so (Zar 1999).

Some generalisations, however, can be made. Consistent across all sites is that fruit are the most frequently consumed food item. This is followed by leaves in every site except the Lopé forest fragment (Tutin 1999). Gautier-Hion (1988) stated that consuming around 100 plant foods was typical for *Cercopithecus* Spp., with around 80% of their diet being acquired from 30 plant species. While this prediction is not supported by all previous studies, the longer the study, the more species were recorded. Shorter studies may miss important but less commonly used species, which may account for lower values observed in some studies (Chapman et al. 2002, Porter et al. 2014). However, as no study reported greater than 85 species, despite durations up to ten years, at seems probable that *C. nictitans* consumes less species than Gautier-Hion (1988) identified as typical.

Location	Author/s	Elevation (MAMSL)	Forest Size	Level of Disturbance	Troop Size	Duration	Variety in diet	Diet (%)	Number primate species	Method
Makandé Forest, Gabon	(Brugiere et al. 2002)	200-350	Large Continuous	Low	11.2 ± 0.3	2 years, 2919 observations	31 families	F 85.7 L 10.3 FL 4.1 - O 0.0	7	Frequency Method
Makokou, Gabon	(Gautier-Hion 1980)	~526	-	-	-	10 years, 100 stomachs	71 species	F 70.48 L 16.63 FL 0.75 A 9.42 O 2.72	-	Stomach contents analysis
Campo Animal Reserve, Cameroon	(Mitani 1991)	100-200	Large	High	16.00 ± 1.01	9 months, 54 observations	17 species	F 80 L 20 - - -	13	Opportunistic sampling along trails
Lopé Reserve, Gabon	(Tutin et al. 1997)	~469	Medium, Core Forest,	Moderate	13.5 (average)	10 years, 162 observations	85 species	F 64.7 L 22.4 FL 9.4 A 3.5 O 0.0	8	Opportunistic sampling
Lopé Reserve, Gabon	(Tutin 1999)	~469	Small fragment, 100-200m from main forest	Moderate	13.5 (average)	17 months, 483 observations	55 parts	F 48 L 17 FL 9 A 24 O 0	8	Instantaneous scan sampling all primates in fragment
Dja Reserve, Cameroon	(Poulsen et al. 2002)	400 to 800	Large Continuous	Low	1-28	5 years, 489 observations	32 species	F 73 L 13.1 FL 7.2 A 2.5 O 4.3	7	Opportunistic sampling along trails of primates and hornbills
NMFP, Nigeria	Current study	1400-1600	Small Fragmented	High	19-30	36 months, 11,467 observations	-	-	6	Instantaneous scan sampling on all behaviours

Table 1. Characteristics of field sites where diet of *C. nictitans* has been investigated, including the current study at NMFP. Includes country locates, sources of information, elevation of field station, forest size and presence of fragmentation where *C. nictitans* studied, level of anthropogenic disturbance reported, either mean troop size observed in forest or range in size of observed troops, variety in diet either as species, families or food part observed being consumed, percentage of **F**ruit, **L**eaves, **FL**owers, **A**rthropods and '**O**ther' foods consumed, number of primates species residing in the forest, and method used to sample diet. An n-dash '-' is used to indicate a value is unknown, as it was not measured or not reported.

The pair of studies from Lopé reserve (Tutin et al. 1997, Tutin 1999) are more directly comparable than the other studies, because of their shared location and measure of food availability. In Lopé reserve there was less fruit available in the fragment than the core forest, and correspondingly *C. nictitans* living in the fragment consumed less fruit than those in the core. They also ate less leaves, instead increasing their consumption of arthropods. Arthropods are an alternative source of protein from seeds and high utilisation by *C. nictitans* may lower its rate of seed predation, and thus increase its suitability as a surrogate disperser. However Lopé reserve is only one data point, and comparisons are confounded by the fact that the majority of feeding observations in the fragment were on solo-males while in the core forest they were on troop males. Studies with results replicating increased arthropodivory with increased scarcity would help validate the finding.

The need for further studies on *C. nictitans* is not limited to confirming the trends seen in the Lopé Reserve studies. None of these studies specifically focused on *C. nictitans*, several are limited in their design in terms determining diet let alone for assessing the role of *C. nictitans* in seed dispersal. Not all studies reported the number of species in diet, or even the proportional contribution of all potential food types, with only some reporting consumption of arthropods or 'other' food types. Nearly all used opportunistic sampling methods. As primate diet and activity can vary with time of day (Clutton-Brock and Harvey 1977, Robinson 1984), studies that do not use full day follows of troops and systematic sampling techniques may misrepresent proportional use of certain items in the monkey's diet (Altmann 1974, Kaplin and William 2013). Similarly, analysis of stomach contents may have bias if stomachs were collected at similar times each day, as well as bias caused by the varying passage times of different food items (Gautier-Hion 1980). Furthermore, all of the previous studies were conducted below 800 MAMSL, potentially missing key difference is diet occurring at higher attitude. Therefore to help gain a better understanding of *C. nictitans* diet, I compared proportional consumption of diet over three years at NMFP, a fragmented, disturbed montane forest In Nigeria. Understanding diet is not only important for the conservation of *C. nictitans* but is also the first step in determining if, as proposed, it may fill a surrogate disperser role in degrade Afromontane forests.

Based on findings from previous studies I predicted that *C. nictitans* living at NMFP would be primarily frugivorous and that in times of scarcity they would increase the relative proportion of arthropods in their diet.

Current study

The purpose of comparing diet over three years was two-fold: Firstly, increasing the duration of the study increases the likelihood that less common species are sampled and thus improves the accuracy of the dietary assessment (Marshall and Wrangham 2007, Setchell and Curtis 2011). These less commonly utilised species which may be important under certain conditions. For example, such as during periods of ecological stress when species may switch diet or habitat, utilising different species and food types (Marshall and Wrangham 2007, Marshall et al. 2009). Secondly, it allows from comparisons between differing levels of food availability, which helps us better understand *C. nictitans* diet, potentially allowing more effective conservation efforts for the species when needed. Such comparisons also help determine the suitability of *C. nictitans* as a 'surrogate disperser' because it helps gauge their ecological flexibility and potential for seed predation. Disturbance and fragmentation have been shown to lower the availability of fleshy fruit, which in turn increases the competition for these resources (Gautier-Hion 1980, Fahrig 2003, Porter et al. 2014). More flexible species can lower the amount of fleshy fruit in their diet by increasing the consumption of more readily available and/or less contested food stuffs (Tutin 1999, Onderdonk and Chapman 2000, Cristobal-Azkarate and Arroyo-Rodriguez 2007). Unlike comparisons among studies, by keeping the site constant I could help control for a number of factors such as disturbance, forest size and fragmentation which may impact on diet composition, while keeping consistent methodology allows for more confident comparisons.

Food availability may vary between and within years for a number of reasons. Food availability can vary between years due to fluctuations in abiotic factors such as rainfall and sunlight (Nilsen and Orcutt 1996). Access to food may be altered due to inter- and intra- specific competition (Whitten 1988, Albert et al. 2014). Or, as in previous studies inter-seasonal variation may occur as was observed in both Lopé studies, Makandé forest, Dja reserve and at Makokou, with lower fruit and higher leaf and seed consumption occurring in periods of scarcity (Gautier-Hion 1980, Tutin, Ham et al. 1997, Tutin 1999, Brugiere, Gautier et al. 2002, Poulsen, Clark et al. 2002). Therefore I compared diet not only between years, but also between seasons, troops and sexes.

Based off previous studies it was predicted that *C. nictitans* diet would be flexible and thus respond by adjusting proportional consumption when placed under stress. Increasing leaf and arthropod consumption in times or positions of relative scarcity.

Variation in food availability

Season

As mentioned above, seasonal fluctuations in fruit abundance are common and were observed in the both studies in Lopé Reserve, as well as at Makandé forest, Dja Reserve and Makokou (Gautier-Hion 1980, Tutin, Ham et al. 1997, Tutin 1999, Brugiere, Gautier et al. 2002, Poulsen, Clark et al. 2002). In all studies where it was discussed, periods of seasonal scarcity were linked to low fruit consumption by *C. nictitans.* A similar pattern of high and low consumption would therefore be expected in *C. nictitans* at NMFP. However in a study on *P. t. ellioti* diet at NMFP reserve, Dutton and Chapman (2015) observed no significant seasonal variation in fruit abundance and consequently no seasonal variation in diet, despite previous studies on *P. troglodytes* in other locations having observed such variation (Basabose 2002, 2004). If there is no seasonal variation in availability then there is no pressure for *C. nictitans* to alter diet, in response to either relatively scarcity of a preferred food or increased competition.

Based on these assumptions I predicted I would observe no difference in *C. nictitans* diet between seasons but within years.

Year

Fruit availability can also vary inter-annually, and this variation has been used to explain variations in *Cercopithecus* spp. diets. Inter-annual variation yypically follow similar patterns to seasonal variation i.e. periods with low fruit availability are associated with periods of low consumption (Irwin et al. 2015). Though not quantified Brugiere et al. (2002) discussed the impact of years of low availability, reporting that in Makandé forest *C. nictitans* adjusted their diet to include more new leaves, as they did with inter-seasonal scarcity. Diet in these 'lean' years (years with lower than average fruit abundance) is important to understand because the quality of the food available during these periods has been proposed to be the limiting factor on primate biomass in a forest (Struhsaker 1997, Chapman and Chapman 1999, Gupta and Chivers 1999, Brugiere et al. 2002). Species consumed in 'lean' years are therefore important to consider in conservation management plans; increased biomass of an effective seed disperser may decrease the cost of forest regeneration (Wunderle Jr 1997).

Similar to previous studies, I hypothesised that there would be variation in fruit availability between years and that periods of scarcity or 'lean' years would have lower fruit consumption i.e. that there would be inter-annual variation in the diet of *C. nictitans*.

Competition

Sex

Intra-specific competition also occurs within primate troops, with males often having access to the best resources due to their larger size (Jones 1980, Albert et al. 2014). Additionally, different ages and sexes of primates have different food requirements resulting from differences in morphology and behaviour. Cords (1986) observed that pregnant female *C. ascanius* and *C. mitis* increased their consumption of arthropods and new leaves, most likely due to the protein requirement of foetal and milk production. Males of the same species tended to eat more fruit and have precedence at feeding times, which allows them to devote more time to vigilance activities (Gautier-Hion 1980, Harrison 1983). Conversely, males ate fewer arthropods than females due to the relatively high handling time compared to other foods (Cords 1986). Though females typically greatly out-number males in *C. nictitans* troops, the effect is less notable over the whole forest population due to the presence of solo-males (Fa et al. 1995). It is therefore important to differentiate the diet of the different sexes, as a troop average would give a biased sample for the species as a whole if significant difference did occur (Gautier-Hion 1988).

Thus I predicted that there would be significant differences in male and female diets, with males consuming a greater amount of fruit than females. I also predicted that this variation would be greatest in periods of lower availability.

Troop

Intra-specific competition is one of the most important determinants of fruit handling and seed dispersal (Whitten 1988, Albert et al. 2014). Competition for resources is highest when dietary overlap is highest, as organisms are competing for access to the same resources (Darwin 1859, Porter et al. 2014). Highest dietary overlap, and thus highest competition, should therefore occur with conspecifics due to shared dietary requirements and behaviour (Hare 2001). In intra-specific competition between troops of conspecifics, larger troops should have a competitive advantage, allowing them to control better quality territories and consume larger amounts of preferred food items, creating intra-specific variation in diet among troops (Whitten 1988, Butynski 1990). In *Cercopithecus* Spp. this has been observed to lead to higher intra- then inter-specific variation in diet within a forest (Tutin, Ham et al. 1997). Variation in food availability within different troops' home ranges also contributes to differences in diet among con-specifics in the same forest, but does not explain all the variation observed (Chapman 1987). If diet varies with troop

size it is probable, that similar to studies of short duration, studies that focus on one troop may miss species consumed by *C. nictitans* leading to inaccurate assessment of diet. This may lead to over or under assessment of value as a seed disperser or of the importance of a food item in a diet.

NMFP contains a number of *C. nictitans* troops of varying size (Gawaisa 2006). I predicted that there would be significant differences between *C. nictitans* troops' diets within a year and that a larger, more competitive troop would consume a greater amount of fruit.

Methods

Field Site

My study was conducted within NMFP, a submontane forest reserve located on the western escarpment of the Mambilla Plateau (7°30 N, 11°30 E), in Taraba State, Nigeria at elevations between 1400-1600 MAMSL. The area of forest within NMFP is approximately 5.3 km^2, surrounded by a number of smaller riparian fragments within a grassland matrix (Chapman and Chapman 2001). Mean monthly minimum and maximum temperatures for the wet and dry seasons are 26 and 13 ° C, and 23 and 16 ° C respectively (Fig 1). Mean annual rainfall is approximately 1,800mm, occurring predominantly between April and October (Nigerian Montane Forest Project Weather data) (Fig 1). In addition to *C. nictitans,* the forest contains five other primate species *Papio anubis* (olive baboon), *C. mona* (mona monkey), *Chlorocebus tantalus* (tantalus monkey), *Colobus guereza occidentalis* (black and white colobus monkey) and *Pan troglodytes ellioti* (Nigerian Cameroon chimpanzee) (Chapman et al. 2004).

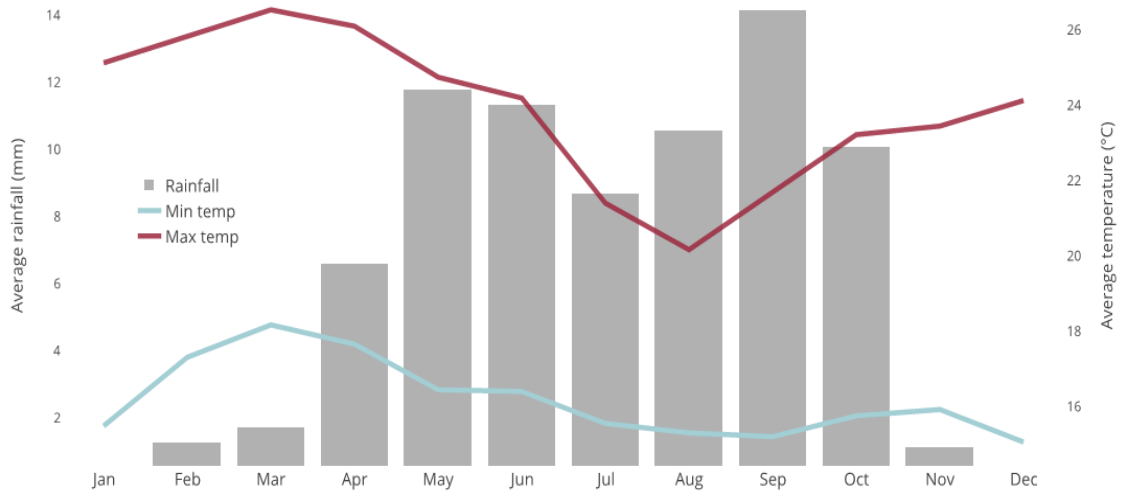

Fig 1. Average mean daily rainfall (mm), minimum temperature (°C) and maximum temperature (°C) for each month at NMFP from January 2006 to March 2014.

Subjects

Behavioural observations were conducted over three years on three different *C. nictitans* troops. The first troop, SGT, was observed between January 2005 and December 2006 while the remaining two troops, BBT and MFT, were observed concurrently between November 2013 and October 2014 inclusive. Due to the seven year gap between observations and low visibility making it difficult to identify individual monkeys, it was not possible to observe SGT in the 2013-2014 season.

SGT, which was not habituated, comprised 24 individuals and was considered representative of other troops in the area (Gawaisa 2006). Observations were conducted for eight hours a day (0600 to 1200 and 1600 to 1800), ten days per month over a 24 month period (January 2005 to December 2006). This resulted in 11,029 individual observations gathered over 240 days or 1920 hours. Data were collected by Stephen Gawaisa with the assistance of a local field assistant Musa Bawuro.

In the 2013 season my observations were focused on two troops of semi-habituated *C. nictitans*, both living in the main forest. MFT had 19 and BBT had 30 members. Observing two troops allowed for a comparison of troops within a year, and provided a more representative sample of *C. nictitans* in the reserve. MFT individuals were physically

smaller than BBT's members, which were the largest observed in the reserve. MFT also had more non-adult members than BBT (six versus three). BBT and MFT demonstrated a notable degree of home range overlap. At least three other *C. nictitans* troops were observed in the vicinity of BBT and MFT during the study, as well as a number of solo-males. Observations were conducted over 487 days (October 2013 to February 2015) between dawn and dusk. This resulted in 6,570 or 109 hours and 30 minutes of observations. Data were collected by three observers in total; from November 2013 through to February 2014 Musa Bawuro, who had continued to observe troops in the inter-study period, and myself, and from February 2014 to October 2014 Musa Bawuro continued with the assistance of a further local field assistant, Thomas Patrick. There was a period of overlap in February in 2014, where all three observers worked concurrently, to help ensure inter-observer reliability.

Behavioural Data

During both study periods observations were conducted using scan sampling (Altmann 1974). In 2005 and 2006 scans were conducted for 15 minutes on the hour. The troop was systematically scanned alternatively from left to right then right to left (Gawaisa 2006). During these scans only one activity was recorded for each member. Scans were conducted from at least 50 m away to minimise disturbance to the troop that could alter their behaviour and a telescope was used to help identify food items. As the length of scan increases so does the likelihood that all individuals will be sampled. Longer inter-observation lengths also ensures that each sample is independent of the previous one, however they decrease the likelihood that rare behaviours will be sampled within a given time period due to fewer observations creating a relatively smaller sample size (Martin and Bateson 1986).

During the 2013-2014 season scans of all visible members of the troop were conducted for one minute at 15 minute intervals. If scans are too close together they can become dependent on preceding scans, leading to intra-specific variation in feeding behaviours being missed. In contrast inter-observation periods of 15 minutes have however been shown to produce scans which are independent of each other for all behaviours except resting (Kaplin and William

2013). One minute was adequate to scan all visible members of the group and minimised the risk of double scoring an individual during a scan. Double scoring was a risk due to both poor visibility and being unable to individually identify all members of the troop (Kaplin et al. 1998). This method was systematic and allowed a better estimate of feeding duration than previous methods due to the closer frequency of scans. However the shorter scan times increased the risk of the observer overestimating the occurrence of common or 'loud' behaviours, and underestimating uncommon ones (Martin and Bateson 1986). This was minimised by having two observers and systematically scanning in alternative directions as described above. Scans were conducted using binoculars at distances of approximately 20 to 50 m.

Records were made of the individual's activity or state, and details of the food items consumed. In 2005 and 2006, all items observed being ingested were recorded. Items that constituted less than five percent of the diet were categorised 'other' (stem, bark, fungi, tendrils, honey juice), new leaf (leaf buds) or flowers (orchids, flower buds). As most arthropods were unable to be identified, they were grouped as one category. Likewise difficulty in differentiating between ripe and unripe fruits, and mature and new leaves led to them being grouped. During 2013-2014 food items were categorised into the six groups: fruit, new leaves, old leaves, flowers, arthropods or 'other'. For analysis leaves were grouped to keep consistency between years. As individual identity of the monkeys was not discernible, age and sex were recorded. Individuals were placed in one of five classes; adult female, adult male, sub-adult, juvenile and infant, with membership in a class being determined by size.

Weather Data

Weather data were sourced from ongoing observations at NMFP. These have been collected manually since January 2006 however and were augmented in 2009 with the addition of an automated Campbell data logger. The weather station takes recordings every fifteen seconds which are averaged after ten minutes. Variables recorded include average photosynthetic radiation (mV), maximum wind speed (ms^{-1}), average air temperature (°C), barometric

pressure (hPa), accumulated rainfall (mm), and soil temperature (°C). Due to this change in recording method, analysis and comparisons with 2006 data are limited to average daily rainfall (mm), and maximum and minimum daily air temperature (°C) whereas comparisons for 2013-2014 also include mean daily air temperature (°C), and minimum, maximum and mean daily soil temperature (°C). Including 2005 weather data in analyses was not possible as data were not collected during this period.

Food Availability

Food availability was defined as abundance of flowers, fruit and leaves in all stages of maturity along established phenology transects. These items constituted 94% of diet in 2005-2006, the remaining 6% was predominantly made up of arthropods, the availability of which was too difficult to monitor with available resources (Gawaisa 2006). Food availability was determined using phenological records from 807 trees, representing at least 89 species, collected along 24 transects over 18.8 km (4.0 m wide = 75,200 m^2) distributed throughout the forest (Dutton and Chapman 2015). Transects have been surveyed once a month since 2003 and records include trees species, life status (alive, dead, coppice), diameter at breast height (DBH) and abundance of new leaves, flower buds, flowers, immature fruit and mature fruit (henceforth collectively called food items). Food items were scored on a five point scale representing their percentage of crown coverage. A score of '0' indicated complete absence, '1' coverage up to 25%, '2' 25 to 50% coverage, '3' 50 to 75% and '4' 75 to 100% (Dutton and Chapman 2015). As individual trees are of varying size, an analogue of abundance was then calculated by multiplying this score with the basal area of individual trees. As a measure of true abundance would have been difficult to measure and impossible to determine for historical data, this instead created an index based on the relationship between basal area and crown size, and the relationship of scores to percentage crown coverage (Setchell and Curtis 2011). It allows for the comparison of relative abundance of food items and food availability between different time periods, in turn creating a consistent measure of food availability for both the earlier 2005 and 2006 data and the recent 2013-2014 data.

Statistical Analysis

Diet of C. nictitans

The diet of C. nictitans was classified by categorisation into five food types (flowers, fruit, arthropods, leaves and other) in terms of the proportion of independent feeding observations spent eating that category over the time period of interest (Chapman 1987). Classification was done for all observations of focal troop regardless of age or sex class, as well as for adult female and males for each year, and for the wet and dry season of each year.

To assess the factors that influence proportional consumption of the different food types I ran a quasi-Poisson Generalised Linear Model (GLM) testing the effect of year (2005, 2006, 2013-2014), season (wet, dry), sex (male, female), food type (fruit, leaves, arthropods, other) and all possible interactions of these. The response variable was transformed using an arcsine transformation to account for the use of proportion data. Model selection was then conducted using stepwise removal of terms and comparison of AIC score (Crawley 2012).

Following this, I conducted a planned contrast of seasonal consumption by sex between years. This allowed me to test the hypothesis that there would be significant differences between 'lean' and 'normal' years but not between the two 'normal' years. To assess this I used pairwise Chi-squared tests for goodness of fit with a False Discovery Rate (FDR) correction. FDR was suitable as the data were normally distributed and showed positive regression dependency (Benjamini and Yekutieli 2001). I used the same method to investigate a second planned contrast between sexes within years, in which I compared each sex/season pair (female/wet, female/dry, male/wet and male/dry). This was to test the hypothesis that female's diet would be significantly different from the corresponding male diet in 'lean' years but not in 'average' years.

Variability between troops

To investigate variation in diet between troops within a year I used only data from 2013-2014. Observations from 2005 and 2006 were excluded as they were of one troop and on a different temporal scale. I compared the observed

diet of troop BBT with the expected diet from observations of troop MFT using a Chi-square test with flowers, fruit, new leaves, old leaves and arthropods as the food type categories. 'Other' was excluded as a food type in the analysis due to the low (< 5) number of observations (Zar 1999).

Comparison food availability between years

I used pair-wise Wilcoxon signed-rank tests to determine if availability of food in 2005, 2006 or 2013 was statistically significantly different from the average availability from 2005 to 2013. Wilcoxon tests were suitable as the inclusion of the years of interest in the calculation of average availability meant that I violated the assumption of independence, thus a parametric test would be unsuitable. I FDR to correct for multiple comparisons. Reported p-values are post-adjustment. This allowed me to test the hypothesis that 2013 was a 'lean year', having lower availability of potential food items, and that 2005 and 2006 represented 'normal' years, with average availability.

To determine if certain food types varied more than others between years, and thus had a greater impact on the occurrence of 'lean' years, I ran a MANOVA with a Pillai-Bartlett test. I used year as the explanatory variable and abundance of measured food items as the response variables. A MANOVA was suitable as pairwise correlations showed that availability of food types was correlated, as would be expected given that measurements of all variables were determined using the same trees (O'Brien and Kaiser 1985). Abundance was calculated, as explained above, using basal area and phenology scores from trees along established phenology transects, for this analysis only data from 2005 to 2014 were used.

As C. nictitans was observed utilising only a subset of the available woody species (30 of 89 species in phenology transects) I ran a second MANOVA using the same variables but including only the known food species (Table 1). This framed availability in terms of the C. nictitans diet which potentially could contain species which have more or less reliable food availability between years than the average of species in the forest.

To quantify variety of species available each year, the number of species with a phenology score greater than one in each month was counted and compared between years using Kruskal-Wallis rank sum tests. Comparisons were made between the number of species producing any measured food type, as well as for each of the food item.

Influence of variation in weather between years

Informal observations indicated 2013 and 2014 may have been 'lean' years, with lower overall food availability than average. Potential causes of this could be variation in weather variables, such as amount of sunlight and rainfall (Nilsen and Orcutt 1996). To investigate if observed weather variables differed between years (and thus may have influenced food availability) I used Multivariate Analysis of Variance (MANOVA) with a Pillai-Bartlett test. A MANOVA allows for the determination of whether an independent variable(s) has a significant effect on dependent variables while controlling for correlation. A number of observed weather variables were by their very nature both correlated and of interest and thus MANOVA was the most suitable analysis as it allowed analysis of all variables of interest without introducing error due to multiple testing (O'Brien and Kaiser 1985). For MANOVA, Hand and Taylor (1987) recommend Pillai-Bartlett over other test statistics as it is robust to assumptions.

As the introduction of automated data collection introduced further variables of interest I performed two separate MANOVAs. The first compared 2013-2014 weather variables with average values calculated using data from 2009 to 2014 to determine if 2013-2014 was significantly different than average. The second MANOVA compared 2006, 2013-2014 and the average data across all available years to see if the years differed from each other and if 2006 was different from averages. As this analysis used less variables than the first it was not used to investigate if 2013-2014 was different from averages as the first analysis gave a more complete picture.

For the first analysis, in which I compared 2013-2014 weather variables with average values, response variables were minimum and maximum monthly soil temperature (°C), mean daily rainfall (mm), and maximum and minimum monthly air temperature (°C). Power can decrease in MANOVA if factors are too highly correlated, therefore mean air

and soil temperatures were excluded from the analysis because they were too closely correlated with their respective minimum and maximum temperatures (O'Brien and Kaiser 1985).

For the second analysis, comparing 2006 to average and 2013-2014 data, maximum and minimum air temperature and rainfall were the only response variables included. This was due to their being the only variables measured prior to 2009 i.e. only data available for 2006. 2005 was excluded as rainfall data were not available.

Following both MANOVAs, I tested each of the dependent variables using univariate ANOVAs with a Bonferroni correction to see how they differed between years and from average of all years. I choose to correct for multiple testing using the Bonferroni method as it is highly conservative, minimising type I error but increasing type II (Rice 1989). As data were an amalgamation of two collection methods, the likelihood of type I error was increased, necessitating a conservative approach.

Influence of variation in weather between years

I tested the correlation of monthly availability of food items and total food availability (as defined above) with monthly rainfall, maximum and minimum temperatures for 2006, 2014 and average yearly data using cor.test. This tested dependence between each of food and weather variables and indicated the direction and strength of the trend. I then corrected for multiple comparisons using Benjamini and Hochberg's (1995) method to control for false discovery rate (FDR).

Results

Diet

Number of species

In total *C. nictitans* was observed consuming at least 32 different species (Table 2). Of theses they consumed 29 species in 2005, 23 in 2006, and 20 in 2013-2014 (Table 3). Overall, *C. nictitans* were observed eating 73 plant parts over the three years of observation. This included 19 species of flowers, 25 species fruit and 28 species leaves. This excludes unknown species and only includes one non-woody species, *Landolphia buchananii,* due to it both being identified and making up more than 1% of the diet. Unknown non-woody species made up less than 1% of observations, with total unknown species making up 4% of feeding observations.

	Year		
Species	2005	2006	2013-2014
Albizia gummifera	1.34	0.16	0.47
Anthonotha noldeae	9.14	12.01	10.98
Beilschmiedia mannii	-	-	1.03
Celtis gomphophylla	7.02	12.78	6.19
Chrysophyllum albidum	0.28	0.68	0.40
Cordia millenii	-	-	0.02
Croton macrostachyus	0.71	-	-
Deinbollia Sp.	0.12	1.89	1.13
Entandrophragma angolense	0.08	-	0.03
Eugenia gilgii	0.07	-	-
Ficus Spp.	40.14	26.24	37.65
Isolona cf *deightonii*	5.27	6.20	0.01
Landolphia buchananii	4.11	-	0.39
Lannea barteri	0.46	0.23	-
Memecylon afzelii	-	0.07	-
Newtonia buchananii	0.29	0.30	0.08
Parkia filicoidea	1.15	1.54	3.64
Polyscias fulva	1.15	1.42	2.80
Pouteria altissima	12.82	16.12	34.46
Pterygota mildbraedii	0.98	0.44	-
Rauvolfia vomitoria	0.53	-	-
Rothmannia urcelliformis	0.40	0.30	-
Santiria trimera	3.43	7.77	0.96
Schefflera abyssinica	0.21	0.07	-
Strombosia scheffleri	2.46	1.17	1.40
Symphonia globulifera	1.43	0.16	0.01
Syzygium guineense	0.05	-	-
Tabernaemontana contorta	0.36	-	-
Trichilia welwitschii	3.18	1.98	-
Trilepisium madagascariense	0.03	0.44	0.08
Uapaca Sp.	0.03	-	-
Unknown	2.84	3.17	0.19

Table 1. Proportional representation of known food species in *C. nictitans* diet in 2005, 2006 and between November 2013 and October 2014. Based on independent feeding observations in each year. A n-dash '-' is used to indicate that a species was not in the diet that year.

	Food Part		
Species	Flowers	Fruit	Leaves
Albizia gummifera		X	X
Anthonotha noldeae	X	X	X
Beilschmiedia mannii		X	X
Celtis gomphophylla	X	X	X
Chrysophyllum albidum		X	X
Cordia millenii		X	X
Croton macrostachyus		X	
Deinbollia sp.	X	X	X
Entandrophragma angolense	X		X
Eugenia gilgii		X	X
Ficus spp.		X	X
Isolona cf *deightonii*	X	X	X
Landolphia buchananii	X	X	X
Lannea barteri		X	X
Memecylon afzelii			X
Newtonia buchananii		X	X
Parkia filicoidea	X	X	X
Polyscias fulva	X	X	X
Pouteria altissima	X	X	X
Pterygota mildbraedii			X
Rauvolfia vomitoria	X	X	X
Rothmannia urcelliformis		X	X
Santiria trimera	X	X	X
Schefflera abyssinica	X		X
Strombosia scheffleri	X	X	X
Symphonia globulifera	X	X	
Syzygium guineense		X	
Tabernaemontana contorta		X	X
Trichilia welwitschii	X	X	X
Trilepisium madagascariense	X	X	X
Uapaca sp.	X	X	X
Total	19	25	28

Table 3. Food items consumed by *C. nictitans* over three years of observation at NMFP, excluding unknown species and non-woody species which constituted less than 1% of the diet over the three years. Each food part includes all stages of maturity for that food item.

Composition

Overall fruit comprised 50.83% of the diet, leaves 34.09%, flowers 6.17%, arthropods 3.31% and 'other' 2.60% (Table 4). This however varied with year and sex (Fig 2). In all years fruit and leaves were the two most consumed food types. In 2005 and 2006 'fruit' had the highest proportional consumption, with highest fruit consumption observed in 2005. Lowest fruit consumption occurred in 2013-2014 and unlike the other two years it was not the most consumed food type, with leaves instead ranking first (Table 4). Lowest leaf consumption occurred in 2005.

	Food type				
	Flowers	Fruit	Arthropods	Leaves	Other
2005	6.08	57.21	2.14	33.21	1.38
2006	4.65	49.41	3.03	37.82	5.09
2013	4.69	38.29	8.07	48.95	<1
Combined	6.17	50.83	3.31	34.09	2.60

Table 4. Percentage of five food items in the diet of observed *C. nictitans* at NMFP in 2005, 2006, November 2013- October 2014 and the average of the three time periods (combined). The most consumed food stuff, as determined by highest relative percentage of independent feeding observations, is shaded grey.

Did diet differ between troops in 2013-14?

There was a significant difference in the diet of the two troops, BBT and MFT, during 2013-2014 ($\chi^2 = 76.7259$, $p < 0.001$). MFT, the smaller of the two troops, was more folivorous than BBT (53% and 43% respectively) and consumed a relatively lower amount of all other food types (Fig 3). Though BBT consumed less leaves overall, new leaves constituted twice as much of its diet than of MFTs (3% and 6% respectively) (Fig 3).

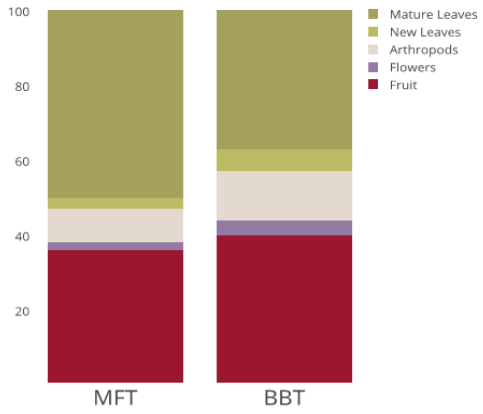

Fig 3. Comparison of the diet of all individuals in two *C. nictitans* troops living in NMFP between November 2013 and October 2014 (inclusive). Values represent the percentage of independent feeding observations on that food type. 'Other' was excluded as it represented <1% of either troops diets.

Did male and female diet differ?

Male and female diet differed significantly (X^2 = 13.501, p = 0.0091), with the largest differences seen in proportional consumption of leaves and arthropods. Females ate more leaves, and fewer arthropods than males (Fig 2). Despite the significant difference, males and females ate comparable amounts of fruit, which comprised around half of independent feeding observations in both sexes. They also ate similar amounts of flowers, and 'other' food types with less than 1% difference between the sexes.

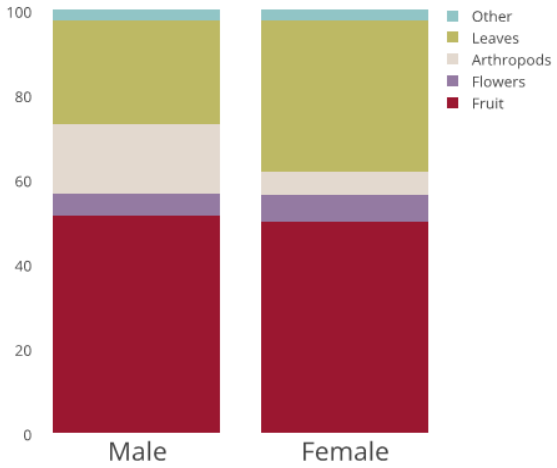

Fig 2. Proportional consumption of five food types (flowers, fruit, arthropods, leaves, other) by adult female and male *C. nictitans* in 2005, 2006, 2013-2014 (2013 in figure) and for the average of 2005, 2006 and 2013-2014. Each food type combines all stages of maturity for that food type.

Did female and male diet differ in all seasons?

Male and female *C. nictitans* did not however consume significantly different diets during all seasons (Fig 4). While their diets differed significantly from each other during all three observed wet seasons; 2005 (X^2 = 26.372, p = 0.002), 2006 (X^2 = 16.554, p = 0.014) and 2013 (X^2 = 169.872, p = 0.006). They were only significantly different during the 2013-2014 dry season (X^2 = 103.103, p = 0.004).

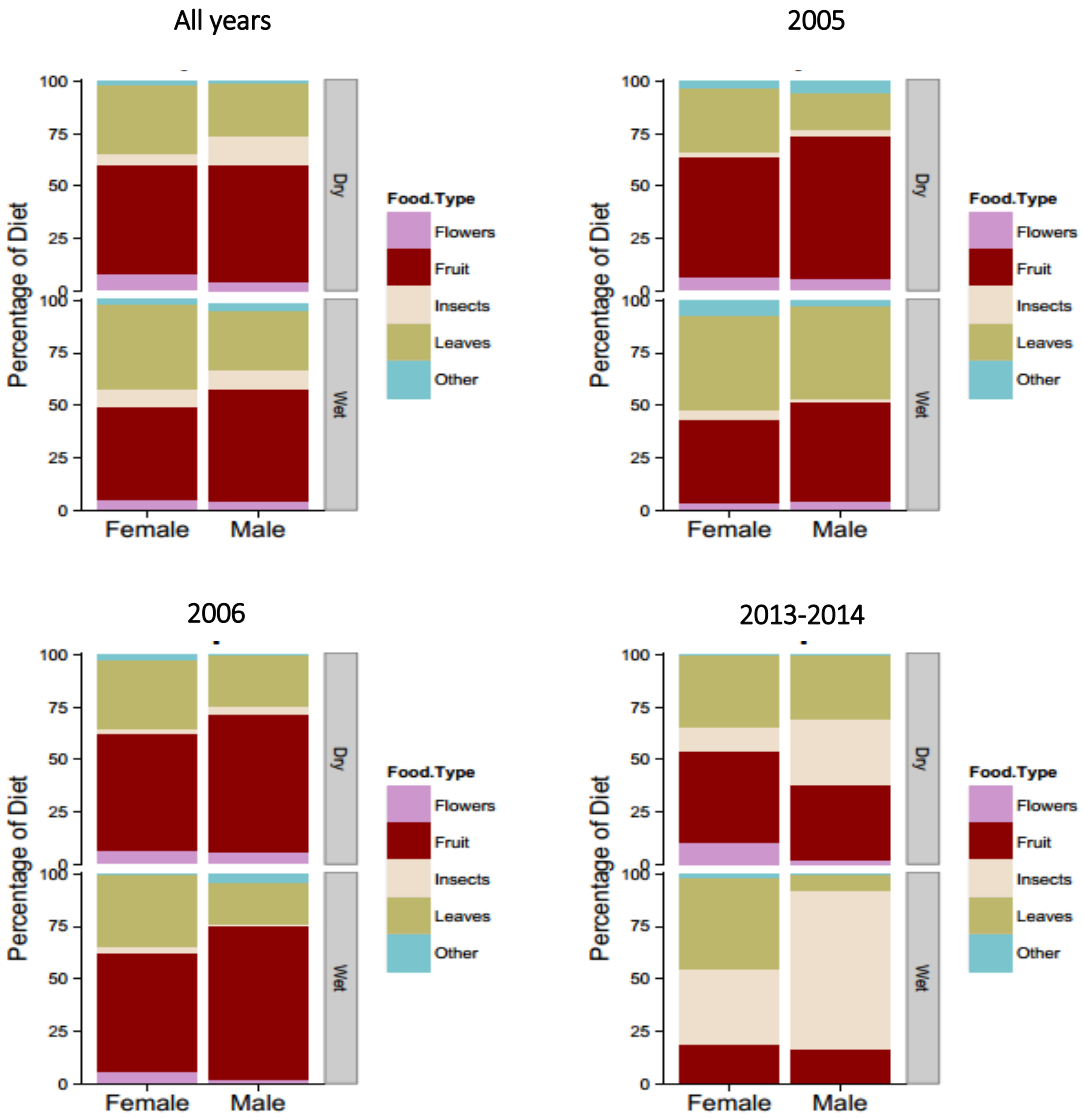

Fig 4. Percentage consumption of five food types (flowers, fruit, arthropods, leaves, other) by adult female and male *C. nictitans* in 2005, 2006, 2013-2014 (2013 in figure) and for the average of 2005, 2006 and 2013-2014 in the wet and dry season. Each food type combines all stages of maturity for that food type.

Was male diet more similar to females in the same or opposing season within a year?

All comparisons of male and female diet between seasons within a year were significantly different (Table 5) except for 2005 (X^2 = 5.287, p = 0.182). This indicated during 2005 male diet in the wet season was more similar to females in the dry season than it was to female diet in the corresponding wet season.

		Year		
		2005	2006	2013
Sex/season pairs	Female/Wet & Male/Wet	p = 0.002 * (*26.372*)	p = 0.014 * (*16.554*)	p = 0.006 * (*169.872*)
	Female/Dry & Male/Dry	p = 0.299 (*3.882*)	p = 0.3363 (*3.382*)	p = 0.004 * (103.103)
	Female/Wet & Female/Dry	v0.003 * (*15.818*)	p = 0.002 * (*16.853*)	p < 0.001 * (*61.040*)
	Male/Wet & Male/Dry	p < 0.001 * (*26.905*)	p < 0.001 * (*41.960*)	p = 0.397 (*4.066*)
	Female/Dry & Male/Wet	p = 0.182 (*5.287*)	p = 0.003 * (30.303)	p = 0.006 * (13.99)
	Female/Wet & Male/Dry	p = 0.010 * (*12.409*)	p = 0.030 * (*90.622*)	p = 0.012 * (1857.33)

Table 5. Chi-square test result for comparisons of proportional consumption on five food types (fruit, leaves, flowers, arthropods other) of two sex/season subsets of observed *C. nictitans* in NMFP within years. The top value is the p value after False Discovery Rate correction and the value beneath the X^2 value. An asterisks (*) is used to denote significance at α = 0.05.

Was diet different between years?

Female and male diet, during both seasons was significantly different between the 'lean' year (2013-2014) compared with both the 'average' years (2005 and 2006). When the two 'average' years were compared, only male diet in the wet season was significantly different. As above, all reported *p*-values are after FDR correction (Table 6).

		Year pair		
		2005 – 2006	2005 – 2013	2006 – 2013
Sex/season	Female/Wet	$p = 0.137$ (*5.95*)	$p < 0.001$ * (*313.87*)	$p < 0.001$ * (*203.82*)
	Female/Dry	$p = 0.999$ (*0.45*)	$p < 0.001$ * (*73.82*)	$p < 0.001$ * (*50.55*)
	Male/Wet	$p < 0.001$ * (*28.61*)	$p = 0.001$ * (*7721.63*)	$p < 0.001$ * (*5533.51*)
	Male/Dry	$p = 0.948$ (*0.36*)	$p < 0.001$ * (*291.21*)	$p < 0.001$ * (*368.8*)

Table 6. Chi-square test result for comparisons of proportional consumption on five food types (fruit, leaves, flowers, arthropods other) by sex/season subsets of observed *C. nictitans* in NMFP between years. The top value is the *p* value after FDR correction and the value beneath the X^2 value. An asterisks (*) is used to denote significance at $\alpha = 0.05$

How did male and female diet differ between years?

Both female and male *C. nictitans* demonstrated differences in the proportional consumption of food parts in both the wet and dry season between years (Fig 5). During the wet season females ate a lower proportion of flowers, fruit and 'other' food types, as well as more arthropods in 2013-2014 than both 2005 and 2006 (Table 7). They also ate a lower proportion of leaves in 2013-14 than they did in 2006, but more than they did in 2005. The same pattern was seen in the males' diet in the wet season of 2013-2014 when compared with the 2005 and 2006 wet seasons. Males in 2006 ate a lower proportion of flowers, fruit and 'other' food types and more leaves and arthropods than those in 2005.

During the 2013-2014 dry season females spent a higher proportion of time eating flowers and arthropods, and less eating 'other' food types compared to 2005 and 2006. Over both seasons in 2013-2014 they spent a lower proportion of time consuming fruit and more time eating leaves than 2006, and compared with 2005 they spent a higher proportion of time eating fruit and lower eating leaves. During the 2013-2014 dry season males ate a lower proportion of all food types except 'arthropods' compared to both 2005 and 2006. They ate more arthropods than they ate in either of the other years (Table 7).

a)	Female					Male				
Food Type	Flowers	Fruit	Arth.	Leaves	Other	Flowers	Fruit	Arth.	Leaves	Other
2005 *	5.7	56.1	3.7	34.1	0.3	2.0	73.1	0.7	20.1	4.03
2006 *	3.4	39.5	5.1	44.5	7.5	4.1	47.9	1.0	44.0	3.0
2013-2014 *	0	18.7	36.1	43.4	1.9	0	16.7	75.0	8.3	0

b)	Female					Male				
	Flowers	Fruit	Arth.	Leaves	Other	Flowers	Fruit	Arth.	Leaves	Other
2005	6.7	56.0	1.6	32.8	3.0	6.0	66.0	3.1	24.8	0.2
2006	6.6	57.4	2.1	30.8	3.1	5.3	68.8	2.5	17.7	5.6
2013-2014 *	10.8	42.9	11.5	34.8	0.0	1.6	35.7	32.0	30.7	0

Table 7. Percentage of independent feeding observations on five food types (flowers, fruit, arthropods, leaves, 'other') by adult female and male *C. nictitans* at NMFP in 2005, 2006, 2013-2014 in the **a)** wet and **b)** dry season. Each food type combines all stages of maturity for that food type. The highest value for each sex in each season is shaded grey. Years where male and female diet was found to be significantly different using chi-square tests, at $\alpha = 0.05$ are marked with and asterisks "*".

Was fruit the most consumed food type?

These difference in food consumption between years are reflected in the different feeding strategies during the wet seasons. In 2005 (an 'average' year) both females and males were predominantly frugivorous, with over half of independent feeding observation occurring on fruit. This was also true of males in 2006 ('average' year) whereas females spent a slightly higher proportion of time feeding on leaves than they did fruit. In 2013-2014 ('lean year')

similar to 2006, females spent a higher proportion of time feeding on leaves than any other food types. Unlike 2006 however, females spent a greater proportion of time consuming arthropods than they did fruit, the latter of which made up less than a fifth of their diet. For males in both 2005 and 2006 fruit constituted the highest proportion of observations, whereas males in 2013-2014 were predominantly arthopodviourous. A further difference between years was that during the 2013-2014 wet season neither male nor female *C. nictitans* were observed to consume 'flowers', which was in contrast to both other years. These differences were not observed during the dry season where in all years both males and females were predominantly frugivourous. However in 2013-2014 dry season male feeding observations were divided approximately into thirds amongst 'fruit', 'leaves' and 'arthropods' with only 5% difference between the highest and lowest value.

How did female and male diets differ?

In all seasons males spent a smaller proportion of time feeding on leaves than females and throughout 2005 and 2006 they spent a greater proportion of time feeding on fruit than females. In contrast however, in 2013-2014 they spent comparatively less time consuming fruit than females, instead spending a greater proportion of time feeding on arthropods. In 2005, males spent less time feeding on both flowers and arthropods. Similarly in 2006 males spent less time feeding on arthropods but also 'other' than females. Males and females ate an equivalent amount of 'other' food types in 2005 and of flowers in 2006 and 2013-2014 (Table XX).

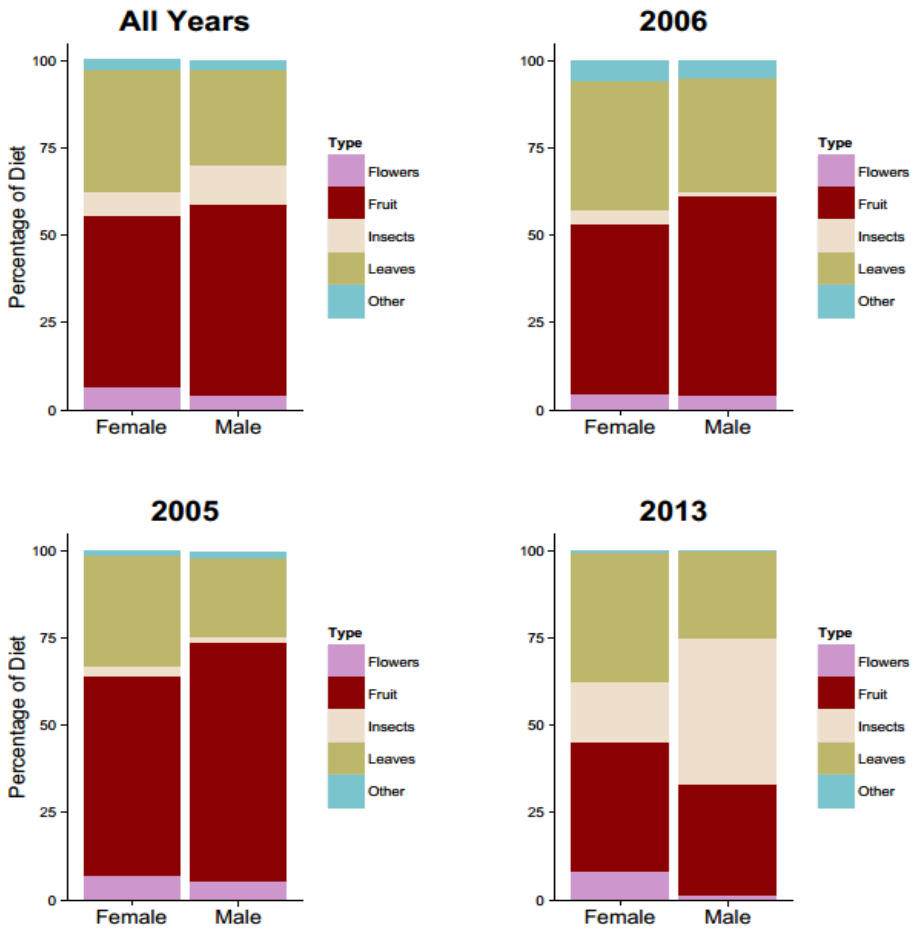

Fig 5. Proportional consumption of five food types (flowers, fruit, arthropods/insects, leaves, other) by adult female and male *C. nictitans* in 2005, 2006, 2013-2014 (2013 in figure) and for the average of 2005, 2006 and 2013-2014. Each food type combines all stages of maturity for that food type.

Was male or female diet more variable between years?

The coefficients of variation for food types showed that males had more variability in proportional use among the three years. They showed more variable use of all food types in all seasons except 'other' food types in the wet season. For both males and females the most variability was seen in consumption of 'arthropods' during the wet season. This was also the most variable food type for females in the dry season, whereas males demonstrated most variability in their use of 'other' food types between dry seasons. For both sexes 'leaves' was the least variable food type. It was the least variable for females in both seasons and males in the dry season. Between wet seasons the least variable use for males was observed in fruit consumption (Table 7).

	Wet		Dry	
	Male	Female	Male	Female
Flowers	99.74	94.39	54.36	30.40
Fruit	61.63	49.27	32.28	15.41
Arthropod	167.38	122.04	134.55	110.01
Leaves	75.33	14.02	26.52	6.09
Other	89.27	118.08	163.84	84.78

Table 7. Coefficients of variation in proportion of feeding observations on five food types (Flowers, fruit, arthropod, leaves and 'other') during the wet and dry seasons between three years for male and female *C. nictitans* living at NMFP. Highest value of variation highlighted dark grey and the lowest light grey for each sex within a season.

Food Availability

Total food availability

Total food availability (as calculated from the phenology data described above) varied among years; most were 'average' years while some years produced markedly less food ('lean' years) and others markedly more ('high' production years) (Fig 6). Of the nine years for which data were available, 2005 was the highest in terms of total availability, 2006 fifth and 2013 eighth. These ranks indicate that 2013 may be considered a 'lean' year, 2006 'average' and 2005 'high'. Fluctuations were also observed in availability of individual food items, with an increase in one not necessitating another. In eight years the most available food was new leaves, in the ninth it was immature fruit. Mature fruit was the least available food in seven years, flowers in one and flower buds in another (Fig 6). Though 2005 had highest total availability, it did not have highest availability of all food types with the most notable difference from 2006 being in the availability of new leaves. Compared to the other two years 2013 had lower availability of all food types except immature fruit.

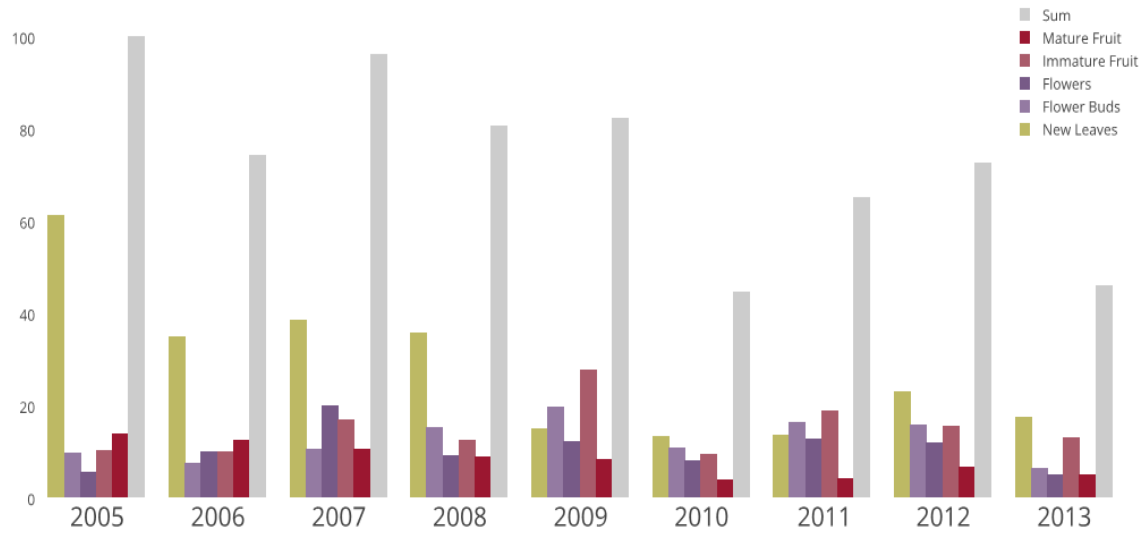

Fig 6. Total food availability (sum of phenology score x basal area) of food types (New Leaves, Flower Buds, Flowers, Immature Fruits, Mature Fruits, Sum of all food types) each year from 2005 to 2013 on the phenology transects (*N* = 807). Values have been standardised.

Was food availability different from average during the three observed years?

The Wilcoxon signed rank test indicated that 2005 (Z = 2.5887, p = 0.0096) and 2013 (Z = -2.1181, p = 0.034) had significantly different availability from average whereas 2006 did not (Z = -1.2551, p = 0.20766). Further supporting that 2013-2014 was a 'lean' year and 2005 a 'high'

At NMFP food availability undergoes monthly cycles with decreasing availability from December to August, then a steady increase from August to December (Fig 7). On average highest total availability occurs in November. This was also observed in 2005 and 2006, however in 2013-2014 highest availability occurred two months earlier, in September. Lowest availability differed in every year, in 2005 in February, 2006 September and 2013 June (Fig 7). In every month except for September, 2013-2014 had lower total food availability than in the average data, 2005 and 2006. The pattern of total availability in 2013-2014 reflects the lower availability of both fruit and new leaves overall (Fig 7) as well as the spike in fruit availability in September seen in 2013 (Fig 7). The lowest total availability in 2006 also coincided with lowest leaf availability.

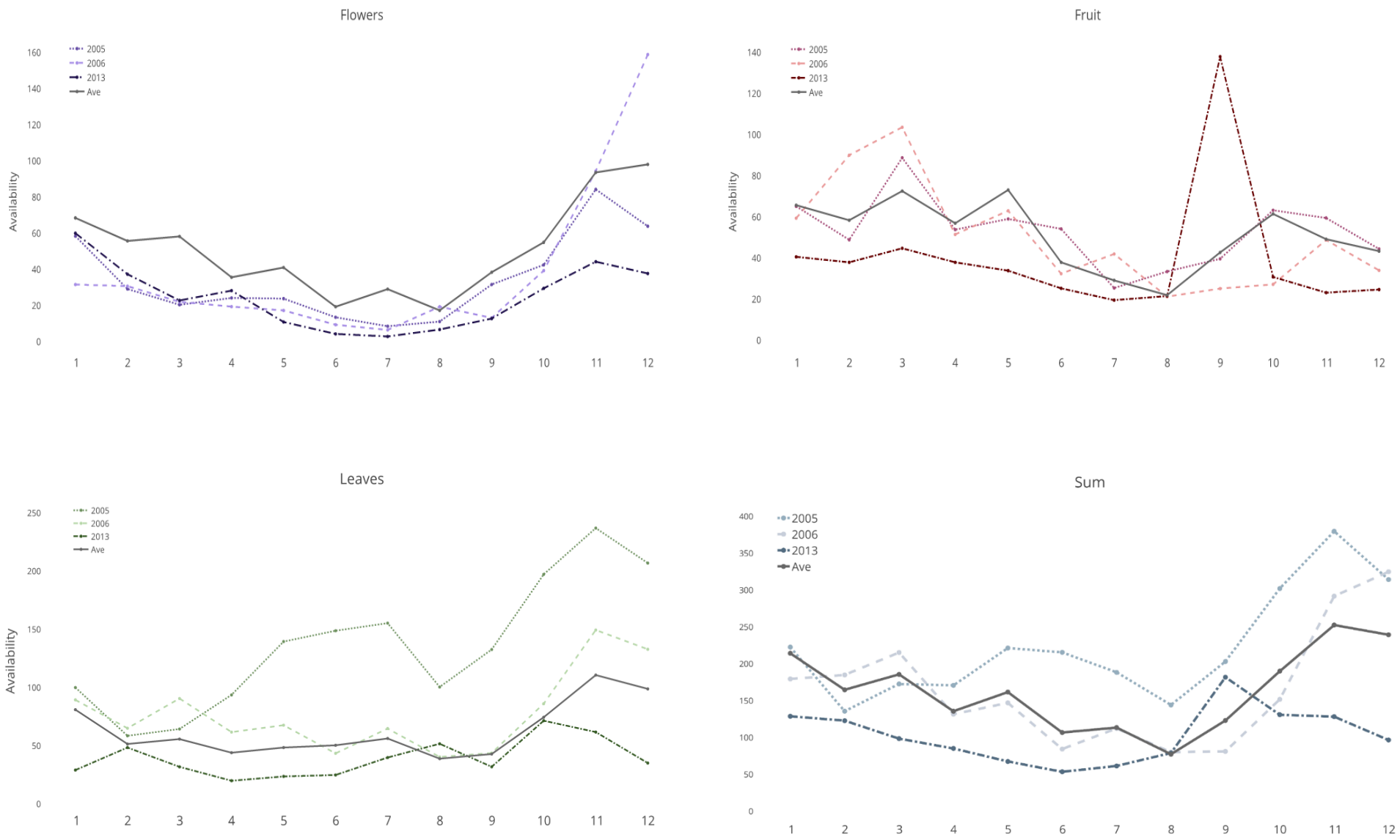

Fig 7. Sum of monthly availability for all species of **a)** flowers and flower buds, **b)** mature and immature fruit, **c)** leaves and **d)** all food parts along the phenology transects at NMFP reserve (*N* = 807) for 2005, 2006, 2013 and the average of 2005 to 2013

Compared to the average data, 2005 and 2006, availability of food types in 2013-2014 demonstrated a more even trend. This is especially evident in availability of fruits where unlike other years, there was no increase in total availability in the dry season. 2006's pattern of availability is more similar to the average data, particularly in displaying the same three peak cycle in the wet season. There were however slightly fewer flowers available in November and December. Food availability in 2005 was similar pattern to 2006 in all food types except for new leaves which were much more available in 2006 than in other years and compared to the average data from 2005 to 2013. This abundance of leaves in mostly responsible for the higher availability of sum of total available food (Fig 7). This may mean that food was more predictable in 2005 and 2006 than 2013-2014 which showed a less 'average' pattern.

Was there different availability of food types between years?

The MANOVA used to explore the availability of food types among years showed that they were significantly different (Pillai's Trace = 0.088593, $F = 2.6645$, $df = (1, 99)$, $p < 0.001$). In particular the *F* tests for new leaves, immature and mature fruit were significant, demonstrating that these food types differed significantly in availability between years (Table 8). The results for flower buds and flowers were not significant, indicating that their availability is more constant over time (Table 8).

The second MANOVA, used to explore whether the availability of species that specifically contribute to the *C. nictitans* diet, varied among years showed that they did (Pillai's Trace = 1.0041, $F = 3.1095$, $df = (8, 99)$, $p < 0.001$). Differences in all food types except flowers were significant (Table 9). The increase in significance, including the new significant difference in flower buds, implies there was greater variability during this period in food availability in species eaten by *C. nictitans* than in all observed tree species. The level of significance for immature fruit however did show a contrary trend to the other food types and was approaching insignificance, indicating it may be more consistent for species in the diet than for overall availability (Table 9).

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		F	*df*	*P*
Food Type	New Leaves	8.1675	(8,99)	< 0.001*
	Flower buds	1.2100	(8,99)	0.301
	Flowers	1.2199	(8,99)	0.295
	Immature Fruit	3.4910	(8,99)	0.001*
	Mature Fruit	2.3048	(8,99)	0.026*

Table 8. Univariate results from *F* test for a MANOVA comparing the availability of five food types (new leaves, flower buds, flowers, immature fruit, mature fruit) for all tree species between years along phenology transects in NMFP in 2005, 2006 and November 2013-October 2014. An asterisks (*) is used to indicate significance at α = 0.05.

		F	*df*	*P*
Food Type	New Leaves	9.5926	(8,99)	< 0.001 *
	Flower buds	2.2083	(8,99)	0.033 *
	Flowers	1.3503	(8,99)	0.228
	Immature Fruit	2.2081	(8,99)	0.0418 *
	Mature Fruit	4.0041	(8,99)	< 0.001 *

Table 9. Univariate results from *F* test for a MANOVA comparing the availability of five food types (new leaves, flower buds, flowers, immature fruit, mature fruit) for tree species in *C. nictitans* diet between years along phenology transects in NMFP in 2005, 2006 and November 2013-October 2014. An asterisks (*) is used to indicate significance at α = 0.05.

Were the same number of food species available each year?

There was a significant difference in the monthly number of species producing a measured food item between years ($H(2) = 7.1534$, $p = 0.02797$). The monthly number of species with new leaves ($H(2) = 8.9972$, $p = 0.01112$), immature ($H(2) = 15.7845$, $p < 0.001$) and mature fruit ($H(2) = 22.33$, $p < 0.001$) was also significantly different. In contrast the number of species producing flower buds ($H(2) = 1.6426$, $p = 0.4399$) or flowers ($H(2) = 1.6194$, $p = 0.445$) was not

(Table 10). Though on average more species produced flowers, flower buds and immature fruit during each month of 2013-2014, other food items were relatively scarce (Fig 8).

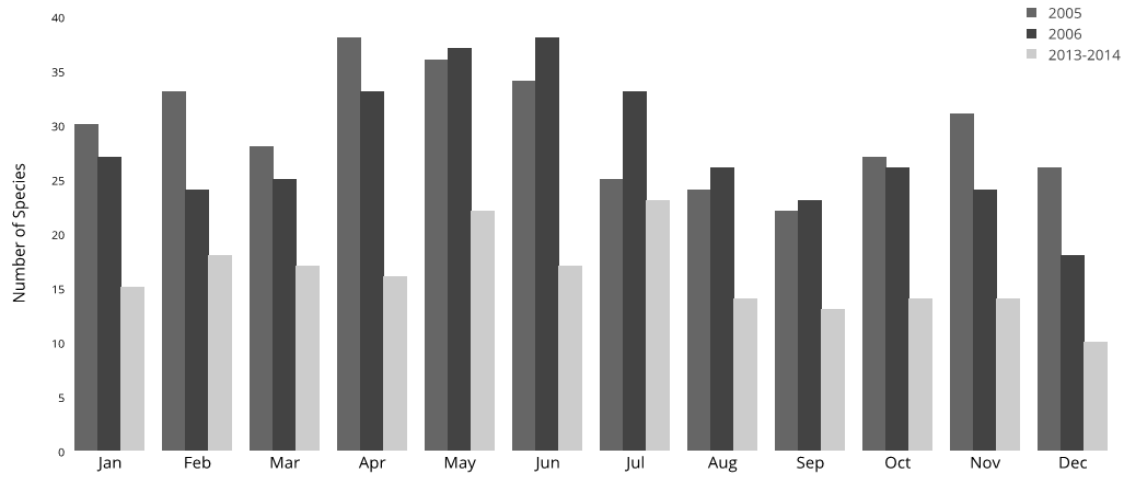


Fig 8. Number of species observed along phenology transects at NMFP with an observable amount of mature fruit each month, in 2005, 2006 and November 2013- October 2014.

		Food Type					
		Total	New Leaves	Immature Fruit	Mature Fruit	Flower Buds	Flowers
Year	2005	75 ± 6.71	61 ± 8.27	21.92 ± 4.94	29.5 ± 5.02	26.08 ± 6.80	18.67 ± 9.32
	2006	70 ± 5.04	54 ± 5.00	22.17 ± 7.21	27.83 ± 6.07	24.5 ± 8.51	20.83 ± 8.09
	2013-2014	68 ± 3.88	49 ± 8.71	35.5 ± 7.18	16.08 ± 3.68	31.53 ± 16.41	26.5 ± 14.27

Table 10. Mean number of species ± standard deviation of species with any observable quantity of five food types (new leaves, immature fruit, mature fruit, flower buds and flowers) available and the with any food types (total) available at NMFP during any month of three years (2005, 2006, November 2013 to October 2014).

Results from analysis supported classification of 2013-2014 as a 'lean' period and 2006 as an 'average' year. Support for 2005 as a high year was more mixed. Overall it had greater than average availability, however most of this was attributable to an increase in availability of new leaves. It had a similar number of species available as 2006, as well as similar levels and in some months lower total availability than average or 2006. Without knowing which species *C. nictitans* consumes or even what proportion food parts contribute to its diet, it is not possible to discern if the

increase in leaves in 2005 would increase food availability from the perspective of *C. nictitans*, given the average levels of availability of other food types. As this study was specifically interested in scarcity, it was also not necessary to determine this. It was sufficient that 2013-2014 was shown to have less total, leaf and mature fruit availability than either other year or average and thus was 'lean'. Hence, for the purposes of this analysis 2005 and 2006 will both be termed 'average'.

Weather

Comparison between years

Was there as difference in weather variables between years?

Overall 2013-2014 was cooler than the average of the eight years of weather data with lower average minimum and maximum monthly air temperatures. Whereas 2006 was warmer and dryer, with notably less days with greater than 6mm of rain. Measured weather variables in 2013-2014 were significantly different from average (Pillai's Trace = 0.60846, $F = 5.5945$, $df = (5, 22)$, $p = 0.003$). Monthly minimum and maximum air temperatures for 2006-2014 are presented in Figures 9 and 10 respectively. There was also a significant multivariate result for the comparison of 2006, 2013-2014 and the average values (Pillai's Trace = 0.48974, $F = 3.459$, $df = (6, 33)$, $p = 0.005$). After Bonferroni correction the alpha for the three univariate tests was $\alpha = 0.017$, this value was used to determine significance. The univariate ANOVAs found that minimum daily air temperature ($F = 5.3365$, $p = 0.010$) and maximum daily air temperature ($F = 5.3365$, $p < 0.001$) were significantly different between years. Daily rainfall however was not ($F = 0.9733$, $p = 0.3884$) (Fig 11).

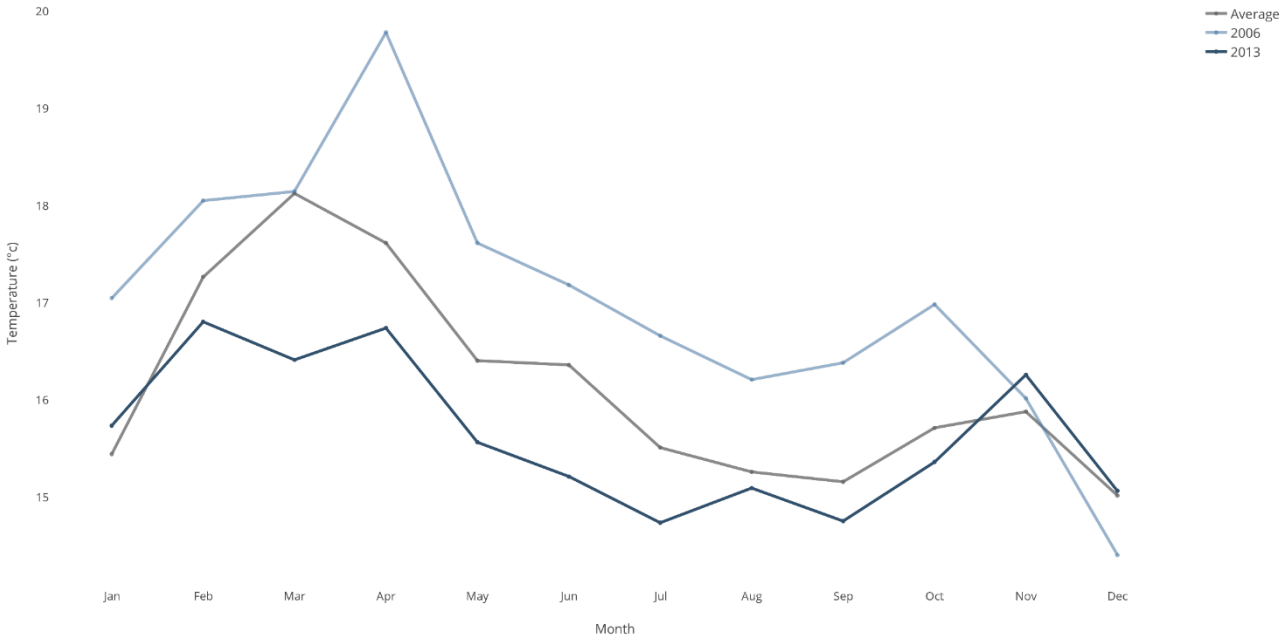


Fig 9. Minimum daily air temperature (°C) for each month at NMFP in 2006, 2013 and the average of 2009 to 2014. Data from 2006 were recorded from a mercury thermometer. Average data and 2013 were recorded using both a mercury thermometer and Campbell data logger.

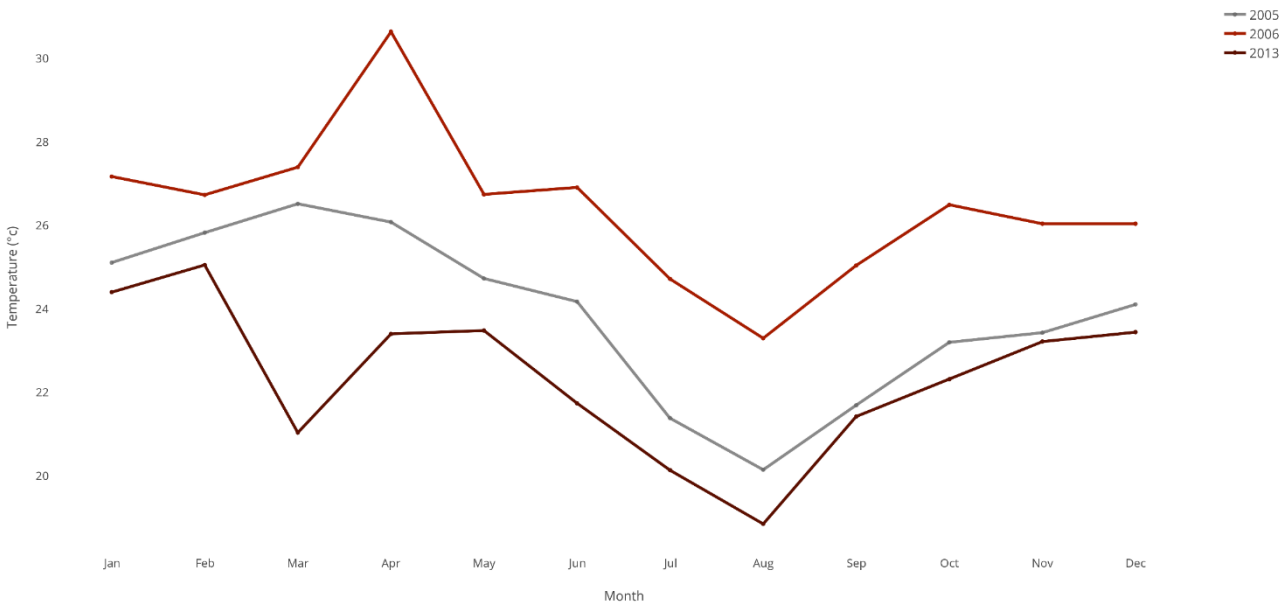


Fig 10. Maximum daily air temperature (°C) for each month at NMFP in 2006, 2013 and the average of 2009 to 2014. Data from 2006 were recorded from a mercury thermometer. Average data and 2013 were recorded using both a mercury thermometer and Campbell data logger.

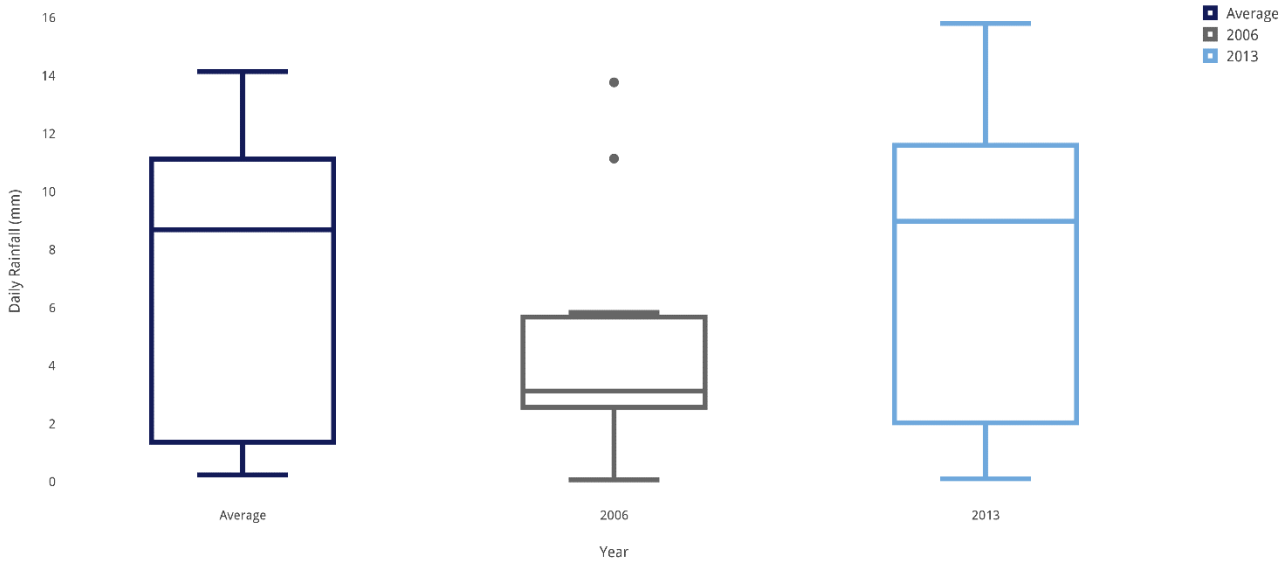


Fig 11. Box plot of average daily airainfall (mm) for each month at NMFP in 2006, 2013 and the average of 2009 to 2014. Data from 2006 was recorded by hand whereas average data and 2013 was recorded by hand and Campbell data logger.

Did weather impact on availability?

There was a strong positive correlation between total food availability and maximum air temperature ($r(34) = 0.420$, $p = 0.01092$) and a strong negative correlation between food availability and rainfall ($r(34) = -0.481$, $p = 0.00295$), but no significant correlation with minimum air temperature ($r(34) = 0.020$, $p = 0.9119$). Weather variables had varying relationships with the availability of the different food types; for example there was significant positive correlation between minimum ($r(34) = 0.591$, $p = 0.03321$) and mature fruit ($r(34) = 0.466$, $p = 0.04177$), and maximum air temperature on new leaves ($r(34) = 0.370$, $p = 0.02653$) and mature fruits ($r(34) = 0.470$, $p = 0.003794$). There was a significant negative correlation between rainfall and new leaves ($r(34) = -0.448$, $p = 0.006097$), flower buds ($r(34) = -0.0506$, $p = 0.00164$) and flowers ($r(34) = -0.499$, $p = 0.001954$) (Table 10).

		Min		Max		Rain		Proportion of independent feeding observations		
		r	*p*	*r*	*p*	*r*	*p*	2006	2013	Ave
Food Type	New leaves	0.0037	0.9828	0.3696	0.02653	-0.4484	0.006010*	0.4693	0.3762	0.4052
	Flower buds	-0.1816	0.289	0.1265	0.4622	-0.5060	0.00164*	0.0982	0.1331	0.1623
	Flowers	-0.2012	0.2383	0.2793	0.09899	-0.4988	0.001954*	0.1322	0.1040	0.1319
	Immature fruit	0.5905	0.03321*	0.0720	0.6766	-0.0550	0.75	0.1323	0.2803	0.1901
	Mature fruit	0.4660	0.00417*	0.4704	0.00379*	0.0562	0.7446	0.1678	0.1062	0.1102
	Total	**0.0191**	**0.9119**	**0.4192**	**0.01092***	**-0.4815**	**0.00295***	1	1	1

Table 10. Pearson's correlations of mean monthly availability of the five food items and sum of all food items (total) with minimum air monthly temperature, maximum air monthly temperature and average daily rainfall in 2006, 2013-14 and the average values from 2009 to 2014 at NMFP. All correlations are to 34 dp. An asterisk (*) is used to indicate significance at α = 0.05. Alongside is the proportion of all independent feeding observations by *C. nictitans* in the location for the same years and average over the three years of observation.

GLM

The variation in the proportion of independent feeding observations on different food types in *C. nictitans* was best described by the *year*, *season*, *food type* and two interaction terms; *season and food type*, and *year and food type*. Within this model the levels of factors that were significant were: 2013 ($p = 0.004$), and four of the five food types; *fruit* ($p < 0.001$), *arthropods* ($p < 0.001$), *leaves* ($p = 0.002$) and '*other*' ($p < 0.001$). The four significant interactions were *2013* with *arthropods* ($p < 0.001$) and *leaves* ($p = 0.006$), *2006* with other ($p = 0.002$), and *wet season* with *arthropods* ($p = 0.020$).

Discussion

In this study I investigated the diet of three troops of *C. nictitans* living in NMFP, Nigeria over three years (one troop in 2005 and 2006, and two troops between November 2013 to October 2014 inclusive). I determined which species made up *C. nictitans* diet and in what proportion different food items contributed. To better understand how *C. nictitans* responds to scarcity, I also investigated how their diet differed by year and what variables may influence this, including weather, season, sex and troop size. Overall the results indicate that *C. nictitans* is a generalist consumer, capable of ecological flexibility in response to varying stressors that cause scarcity. Though fruit comprised the largest proportion of *C. nictitans* diet across the three years, it did not always do so on shorter time scales. In times of most extreme scarcity, *C. nictitans* switched its diet to focus on leaves and arthropods. Such switches may have implications for its potential role as a seed disperser in disturbed Afromontane forests. Overall it appears diet was highly responsive to factors relating to relative abundance, highlighting the importance of comprehensive analysis of diet for both conservation of the species and of those it interacts with.

Variation in weather variables

The analysis of the impact of weather was restricted by technological limitations during 2005 and 2006 when the field site was in its infancy. However it indicated that 2013-2014 variables were significantly different from the average between 2009 and 2014. Furthermore that 2006, 2013-2014 and the average had significantly different minimum and maximum monthly air temperature. With 2006 being warmer than average and 2013-2014 cooler. Though rainfall was not significantly different between years and average, 2006 had less days with high rainfall.

Weather was shown to impact on total food availability as well as on availability of key food parts. As maximum average monthly air temperature increased so did total food availability, increased average monthly rainfall showed the converse effect decreasing total availability. An increase in maximum average monthly air temperature was also correlated with an increase in new leaves and mature fruit, and increased rainfall with decreased availability of new leaves and flower buds. An increase in minimum average monthly air temperature was associated with an increase in immature and mature fruit. The impact of this was seen in the availability of food items between years. In 2013-2014 it was cooler, with lower maximum and minimum average monthly air temperature. There was also lower total food

availability, and lower availability of mature fruit and leaves. In 2006 it was warmer and dryer, as would be predicted it had higher total availability as well as higher leaf and fruit availability.

The correlation of rainfall with food availability but lack of observed difference between years indicate that variation in rainfall instead occurs within years and thus, contrary to prior observations at NMFP, there is seasonal variation in food availability between the wet and dry seasons. This pattern was also observed in graphs of availability and fits with observations in other montane forest which report often higher seasonality than is observed in lowland forests (Williams-Linera 1997, Basabose 2002, O'Driscoll Worman and Chapman 2005). Increased rain in the wet season is associated with a decrease in total availability, and this scarcity likely puts pressure on *C. nictitans.* This may be especially true of the 2013-2014 wet season when the seasonal decrease is combined with the general decrease in availability seen throughout year. If *C. nictitans* diet responds to the pressure of lower availability the greatest variation would be predicted to be observed during this period. Future studies should therefore statistically test for differences in seasonal availability, and if resources allow, difference is food quality with season to investigate how these changes impact on diet.

Variation in food availability

Total food availability varied with time not just on an annual scale but also on a monthly scale. Peak total food availability typically occurs in November, followed by decline, the exact timing of which varied annually but which always occurred during the wet season. This pattern in availability reflects the abundance of leaves, which were typically the most abundant food type. Availability of fruit typically peaked in the transition from the dry to the wet season in March.

Across the three year study there were significant inter-annual differences in total food availability, as well as in availability of new leaves, and both immature and mature fruit. Notably, 2013-2014 had less fruit and leaves available than the other two years and this was more true of species that were present in *C. nictitans* diet than of the other tree species monitored along the phenology transects, which suggests that it is likely that 2013-2014 was a period of high stress.

This was further supported by 2013-2014 showing a significant difference in availability of food types from an ‘average’ year, determined using data from 2005 to 2013. There was no significant difference in 2006, however there was in 2005. There was slightly higher total availability in 2005 than average, there was also notably much higher

availability of new leaves in nearly every month, in some cases over double average or any other year. It is likely that this is the cause of the demonstrated difference.

Between years there was also a statistically significant difference in the total number of species available each month, indicating that not only was there less overall food available in 2013-2014 but that what food was available came from a more limited set of tree species. This does not account for variation in other plant form such as lianas or non-plant foods such as arthropods, but suggests that troops in 2013-2014 had less choice than troops in 2005 and 2006. Specifically, there was less mature fruit and new leaves, the two most consumed food types in the *C. nictitans* diet.

Due to the lower number of species available, lower total food availability and lower availability of both leaves and fruit 2013-2014 was deemed a 'lean' year with lower than average availability. A difference supported by statistical analysis. The remaining two years were classified as 'average' as they showed more typical availability. There is potential that 2005 fell into a third 'high' category, as indicated by the finding it was significantly different from average. Graphical data does not however conclusively support this and as this study's interest was in the impact of low ability it was superfluous to determine the cut off for 'high'. It was sufficient that 2005 and 2006 had both higher and closer to average abundance than 2013-2014.

Diet of *C. nictitans* living in NMFP.

Proportional consumption

As has been found in previous studies, the largest constituent of *C. nictitans'* diet at NMFP was fruit (both immature and mature), making up 50.8% of independent feeding observations over the three years studied. Furthermore, in line with all other studies excluding Tutin's (1999), leaves were the second largest constituent of the *C. nictitans* diet, at 34.1%. Tutin's (1999) study, found instead that arthropods were the second largest constituent. Her study was carried out in a disturbed forest fragment within Lopé forest reserve in Gabon, differing from all others in both focussing on a fragment, rather than on core forest due to the majority of her observations occurring on solo-males. Difference in life histories and thus dietary needs of male and female *C. nictitans* (Gautier-Hion 1980, Harrison 1983) and the possibility that solo males are less competitive individuals forced to utilise the fragment over the higher quality core habitat (Tutin 1999, Gawaisa 2006) may explain the different findings from the Lopé fragment study compared with others, including Tutin et al.'s (1997) study on the nearby core forest at Lopé reserve.

Though fruit was the most consumed food type at NMFP (50.83% of all food types), its contribution to overall diet was markedly less than in the other studies cited in Table 1, where fruit contributed between 64-84% of the total diet excluding Tutin (1999). Tutin (1999) reported only 48.0% of independent feeding observations of *C. nictitans* were on fruit, which was in contrast to the 64.7% observed in a previous study in nearby continuous forest (Tutin et al. 1997). NMFP and Lopé reserves are the two most disturbed habitats in which the diet of *C. nictitans* has been observed to date. It may be that this disturbance has resulted in lower fruit availability compared to more intact sites (Tutin 1999, Cunningham 2000, Cramer et al. 2007) and thus decreased fruit consumption may be a reflection of its scarcity. The potential effect of disturbance on fruit consumption is further supported by the finding that the highest consumption of fruit occurred in the forest with least disturbance; Makandé forest, Gabon, which has only recently become accessible to humans (Brugiere et al. 2002). Here fruit consumption comprised 85.7% of the diet (Brugiere et al. 2002), nearly twice that observed in the Lopé reserve fragment.

At NMFP leaves were consumed at a higher proportional rate than in all previous studies (Table 1) where consumption ranged from 10.3% at Makandé, Gabon (Brugiere et al. 2002) to 22.4% at Lopé Reserve core forest (Tutin et al. 1997). Even this highest value is over 10% lower than the observed 34.1% at NMFP. All the studies cited in Table 1 are from sites below 800 MAMSL. In contrast NMFP is a submontane forest, occurring above 1400 MAMSL. Tropical montane environments tend to have leaves which are more nutritious than those in lowland forests (Waterman et al. 1983, Vitousek and Sanford 1986), so they may represent a higher quality food item in the current study than in studies from lowland sites. Like most *Cercopithecus* Spp.*, C. nictitans* has a simple gut that is not well adapted to digesting leaves (Gautier-Hion 1980), as such leaves are likely to be avoided as they provide little energy or nutrients compared to easily processed food, such as fleshy fruit (Gautier-Hion 1980). However, as the nutrient content of leaves increase, so does the benefit of consuming them, potentially swaying the cost-benefit ratio in their favour (Garber 1987). This advantage of leaves at higher altitude may be even greater when the relatively low availability of fleshy fruit and thus increased travel time to harvest them is considered (Galetti et al. 2000, Hanya et al. 2003, Ganas and Robbins 2005). However until nutrient analysis is undertaken it is not possible to test this hypothesis.

In Tutin (1999) there was a notable increase in the consumption of arthropods compared to all the other studies reported in Table x. In the Lopé fragment arthropods were consumed in 24% of feeding observation, the closest value to this 9.42% at Makokou, Gabon (Gautier-Hion 1980). Lowest reported consumption was at Dja Reserve, Cameroon

with 2.5% (Poulsen et al. 2002). At NMFP, I observed an average proportional consumption of 3.31% over the three years, similar to values at the low end of this range. Consumption however was higher during the 'lean' year, with arthropod consumption increasing to 8.07%. Arthropods are a source of readily available protein (Gautier-Hion 1980) and may therefore represent a fallback food for *C. nictitans* when preferred fleshy fruit is in low abundance, such as during scarce years or in forest fragments (Felton et al. 2009a, Irwin et al. 2015). This is further supported by the variation in arthropod consumption in the two Lopé reserve studies, with lower consumption in the core forest where fruit was reported to be more abundant (Tutin et al. 1997, Tutin 1999). Due to confounding variables and difference in methodology direct comparison between sites in table 1 is not possible, however comparisons between years at NMFP may help determine if arthropods are a fallback food in *C. nictitans* diet.

Number species

Over the three years of the study *C. nictitans* was observed eating 73 different plant parts from 32 different species. This excludes unidentified species which make up 4% of *C. nictitans* diet. Previous studies (Table 1) are inconsistent in the way in which they have reported variety in *C. nictitans* diet, with one (Tutin 1999) reporting parts, one families (Brugiere et al. 2002), and the remainder species (Gautier-Hion 1980, Mitani 1991, Tutin et al. 1997, Poulsen et al. 2002). Number of species varied among studies, with values ranging from 17 at Campo Animal Reserve, Cameroon (Mitani 1991) to 85 in the core forest of Lopé Reserve, Gabon (Tutin et al. 1997). NMFP falls in the middle of this range, along with Dja Reserve in Cameroon, where 32 species were also observed being eaten by *C. nictitans* (Poulsen et al. 2002). Tutin (1999), the only other study to report number of plant parts consumed, found that *C. nictitans* consumed 55 parts, notably less than the 73 observed at NMFP. This fits similar patterns in regards to the Lopé fragment, where *C. nictitans* diet seems relatively impoverished compared to other studies. Without more data however it is erroneous to draw any conclusion. Overall it seems that *C. nictitans* diet at NMFP showed typical breadth of species compared to other studies. However, as in previous studies less than the 100 species predicted by Gautier-Hion (1980) were consumed. This suggests that *C. nictitans* may have a narrower niche width than other *Cercopithecus* spp., however it is outside the scope of this study to test for this.

Cordia millenii

Interestingly, in 2013-2014 *C. nictitans* was observed feeding on *Cordia millenii* (Thia et al 2015). Previous studies and unpublished work at NMFP has indicated that *C. millenii* was only dispersed by *P. troglodytes* (Nishida 2002,

Babweteera 2009, Thia 2014). As a result at NMFP it has been identified that *C. millenii* is experiencing arrested recruitment (Thia 2014). The possibility that *Cercopithecus nictitans* may consume and disperse even a small amount of these seeds thus warrants further investigation, specifically if they move seeds in to suitable microhabitats with both sufficient light and moisture for seedling establishment (Chapman et al. 1999). It is possible that due to previous studies occurring in 'average' or 'high' years this potentially important interaction has been missed.

Summary

It appears that at NMFP *C. nictitans* consume a generalist diet, eating a range of species and utilising all plant parts. Though fruit made up just over half the diet, over a third was leaves. This is fitting with findings from studies of other *Cercopithecus spp.* which indicate a high level of ecological flexibility.

Variation in *C. nictitans* diet

Based off previous studies it was predicted that *C. nictitans* diet would be flexible and thus respond by adjusting proportional consumption when placed under stress, such as low food availability. It was predicted that 'lean' years would demonstrate an increase in insect consumption. As explained above, 2013-2014 was determined to be such a year, whereas 2005 and 2006 were deemed 'average' anf thus serve as a baseline for comparison.

Variation between years

Diet of *C. nictitans* differed in 2013-2014 compared with both 2005 and 2006. In these 'average' years fruit made up approximately half the diet and leaves a third, whereas the pattern was reversed in 2013-2014, with leaves making up just under a half and fruit slightly over a third. In 2005 proportional fruit consumption was slightly higher than 2006 while in 2006, leaves were consumed proportionately more than in 2005. As 2005 had the highest availability overall, this fits with a trend of decreasing fruit consumption and increasing leaf consumption with decreased food availability. A predominantly folivourous diet was not observed in any of the previous studies. This may simply be because the most authors only presented yearly averages which, similar to the average in this study failed to highlight this behaviour. It may also reflect the potentially higher nutritional value of leaves in montane forests (Waterman et al. 1983, Vitousek and Sanford 1986). This is supported by leaf consumption in all three years being higher than that seen in all other studies (Table 1). A further possibility is that the fragmented nature and high disturbance in NMFP meant that there was less fleshy fruit (Tutin 1999, Cunningham 2000, Cramer et al. 2007). Low fruit encounter rates may result in fruit being replaced with the more reliable food types, such as leaves. This pattern was not seen in the Lopé

reserve fragment which had less fruit than the core, this may however be due to dissimilarity between it and the current study such as the differences in troop size, sex ratio and altitude.

During 2013-2014 there was an increase in arthropod consumption to 8.1%, over twice that seen in previous years. This increase fits with predictions, but was still notably lower than that seen between the Lopé core forest and the Lopé fragment where there was an increase in arthropod contribution of an order of magnitude from 2.5% up to 24%. As above this differences in magnitude may be a reflection of difference in study methods and location. My data supports the trend that in periods or locations of scarcity *C. nictitans* increase arthropod consumption, first observed in the Lopé studies (Table 1)

The final notable difference between the 'average' years and 'lean' year was the almost negligible consumption of 'other' food types in 2013-2014. These made up less than 1% of all independent feeding observations in 2013-2014, compared to 5.1% in 2006 and 1.4% in 2005. 'Other' foods such as bark, tree sap and fungi may have higher processing requirement, in terms of harvesting and/or digestion (Irwin et al. 2015). This high processing time, may mean these represent preferred foods which are only harvested when *C. nictitans* has met it dietary requirements and thus can take the time to utilise these more time consuming food items (Winterhalder 1981, Garber 1987, Irwin et al. 2015). To fully understand this would require nutrient analysis foods in *C. nictitans* diet, to determine relative value of food items, and more precise data on food handling and processing time, both of which are beyond the scope of this study. While the presence of 'other' food items was not reported in all previous studies, values from all three years in this study are similar to what values there are from the other sites.

However the possibility that this observed trend is an artefact of human error in interpreting *C. nictitans* behaviour cannot be ruled out. As all observations have been made on non-habituated and semi-habituated troops, observation have had to be made at a distance, often in dense vegetation (Kaplin and William 2013). Moreover different observers can lead to certain behaviours being interpreted differently; for example the removing of bark to consume arthropods living underneath could be read as eating bark, or arthropods, depending on visibility and individual judgement calls. In this study, however, Musa Bawuro conducted observations across all years, helping ensure consistency. So despite a change in second observer between the 'average' years and 'lean' year it seems unlikely that this is the cause of the observed increase in arthropods in the diet during lean years, nor for the increase in 2006.

Variation in diet between sexes

Male and female *C. nictitans* have different life histories and as such are likely to have different dietary requirements (Gautier-Hion 1980, Harrison 1983). They also show sexual dimorphism with the larger males likely having a competitive advantage over the smaller females (Gautier-Hion 1980, Harrison 1983, Porter et al. 2014). Previous studies on *C. nictitans* have not explored this potentiality. Theoretically and from studies compared to females, males should utilise the most readily accessible energy source, such as fruit, allowing them to better perform activities and because their competitive advantage allows them better access to higher quality food (Gautier-Hion 1980, Porter et al. 2014). Females, especially pregnant and lactating females, may have higher consumption of new leaves and arthropods due to the high protein content and their competitive disadvantage (Gautier-Hion 1980, Harrison 1983).

Male and female diet was significantly different, however these differences did not all follow predictions. The most obvious difference was seen in the consumption of leaves and arthropods; females ate a greater proportion of the former and less of the latter. Fruit, which I predicted males would eat more of, was represented in equivalent proportions in the diet of both sexes. The fact that my predictions were not supported may be due to their being based on behaviours of different species, with different dietary requirement and access to different food, or to variables specific to NMFP. As such further studies at different sites would be needed to determine how and potentially why, the differences occur.

Both male and female diet was different in 'lean' years when compared with both 'average' years. This was true of the wet and the dry season. During the 'lean' year there was a decrease in consumption of fruit and increase in consumption of arthropods. This may reflect *C. nictitans* adjusting their diet in response to low fruit availability to maintain a constant protein level, a behaviour that has been noted in *Ateles sp.* (spider monkeys) (Felton et al. 2009a, Felton et al. 2009b). These studies found that in 'lean' years the monkeys would adjust their diet as a means to maintain a constant rate of protein, rather than energy consumption. Increased arthropodivory would be a viable tactic to achieve this. However, the increase at NMFP may also reflect increased availability of arthropods in 2013-2014 resulting in increased encounter rates and neutral selection (Lechowicz 1982, Felton et al. 2009a, Irwin et al. 2015). Without data on arthropod availability and nutrient content of food items it is not possible to determine which possibility, if either, is true. This is an exciting avenue to explore. Moreover if *C. nictitans* responds to scarcity by increasing arthropod consumption to meet protein requirement, as opposed to increasing seed predation, it may be a

more effective seed disperser than previously assumed. This would strengthen the case for its role as a surrogate disperser in disturbed forests. Comparison of sex-season pairs between 2005 and 2006 were not different, except for males in the wet season. This is likely due to the high proportion of fruit males ate during the 2005 wet season. Fruit made up 73.1% of their diet, compared to 47.9% in 2006 and 16.7% in 2013-2014. That five out six comparisons of 'average' years were non-significant, supports the classification of 2005 as an 'average' as opposed to a 'high' year.

Male diet showed greater variability between years than females. This may reflect their competitive advantage allowing them to exploit the most favourable feeding strategy in each of the different years (Jones and Barmuta 1998, Butynski 2002, Albert et al. 2014). In both the wet and dry season the least variable consumed food item between years was leaves, and the most variable, arthropods. Arthropods were most variable for males in the wet season, whereas fruit was most consistent. In the dry season leaves were most consistent and 'other' food types most variable. That lack of variability in leaf consumption likely reflects their more consistent availability, likewise the variability in arthropods their unpredictability. Lower variability in fruit may reflect preference. High variability in arthropods could reflect use as a fallback food, with high utilisation in the 'lean' year causing high overall variability. All these possibilities would be better determined if there was more than three data points and clearly more studies need to be carried out to test some of the ideas presented here.

No previous work has investigated difference is male diet in *C. nictitans* within troops compared with that of solo-males, likely due to solo-males being harder to locate, track and habituate than troops (Setchell and Curtis 2011, Rothman et al. 2012). Males have been reported to make up over a third of a forest's *C. nictitans* populations (Fa et al. 1995). As troop sizes range from 2 up to 60, this suggests there can potentially be large numbers of solo-males within a given forest (Tutin 1999, Chapman et al. 2002, Eckardt and Zuberbühler 2004, Arnold and Zuberbühler 2008, Oates and Groves 2008). As behaviour has been observed to vary in solo-males, for example the increased likelihood of solo-males to cross the hostile matrix to utilise fragments it is important to determine if their diet also differs from females (Tutin 1999, Gawaisa 2006). By focusing on troop, diet is skewed in favour of females, which may be resulting in a false picture of *C. nictitans* diet and thus their role as seed dispersers. It is of note that the previous study with the most disparate results was Tutin (1999), where most observations were on solo-males. The high arthropod consumption by males in the current study reflects and exceeds that seen in the Lopé fragment. However when data was averaged by year and overall, this high arthropods consumption was lost, diluted by inclusion of the females' diet.

Potentially a similar effect happened in the other previous studies, all of which simply averaged males and female data.

Variation in diet between seasons

As mentioned previously, season's may compound the effect of a year with low availability overall, further increasing scarcity. Total availability was lowest in the wet season and thus the largest differences in diet would be expected to occur during the wet season of the 'lean' year, 2013-2014.

In 2013-2014 both female and male diet demonstrated similar adaptations to this lean year. Most notably, both sexes ate a vastly greater proportion of arthropods compared to other years and a lower proportion of fruit (as discussed above). This was most noticeable in the wet season, where male proportional consumption of arthropods was 75.0%, but also occurred in the dry season. This preference for arthropods was even greater than preference for fruit in the two 'average' years, where the highest observed value was 73.1% for males in 2005. The fact that males forwent fruit in favour of arthropods during the lean year of 2013-2014 further emphasises the need for further investigation into *C. nictitans* response to food scarcity. It is important to determine if this pattern holds true over time and if it occurs over a range of habitats.

During the wet season of 2013-2014 males and females both consumed a lower proportion of flowers, fruit and 'other' food types than in average years. They ate a greater proportion of leaves compared to 2005 and less compared to 2006. Presumably reflecting overall food availability, female and males ate more arthropods and leaves in 2006 than 2005, again supporting increased arthropod consumption with decreased food availability.

During both the 2006 and 2013-2014 wet season females consumed more leaves than any other food type, a behaviour that has not been reported before. This preference of leaves by females likely contributed to the higher comparative proportional consumption of leaves in the current study relative to other studies (Table x) As mentioned previously, leaves may be a higher value food item in montane, compared with lowland forests (Waterman et al. 1983, Vitousek and Sanford 1986). It is also possible that the effects of higher altitude (Waterman et al. 1983, Vitousek and Sanford 1986), higher disturbance including greater fragmentation (Gautier-Hion 1980, Fahrig 2003, Porter et al. 2014), and season together led to particularly low fruit availability at NMFP. More consistent methodology among studies is required to investigate this further. If leaf consumption is indeed negatively related to overall food

availability it seems most likely that increased consumption is a reflection of decreased choice, as opposed to preference for leaves. However, relative to previous studies it may be both.

Diet in the wet season was more variable than in the dry. Fruit was always the most consumed food item during the dry season, regardless of year or sex. During the wet season however it was only the most consumed in 2005. Leaves were the most consumed for females in both the 2006 and 2013-2014 wet season, as well as for males in the wet season of 2006. Males in 2013-2014 consumed mostly arthropods. Though not the most consumed item, females also showed a marked increase in arthropod consumption in the 2013-2014 wet season, eating over six times more than females in other years and over three times as much as they ate in the dry season. As the 2013-2014 wet season was the period of greatest scarcity during the study this further supports that arthropods may be a fallback food for *C. nictitans.* Both 2006 and 2013-2014 show decreased fruit consumption in the wet season than in the dry, whereas both males and females in 2005 show the opposite trend. However the difference in consumption for females was a negligible 0.1%. In 2005 there was an increase in leaf availability during the wet season that differed from both the average data and from 2006. It contributed to notably higher total overall availability during this period. That the 2005 wet season is less different from the dry, may reflect this high year-round availability of leaves providing a reliable food source that then allowed for *C. nictitans* to spend time and energy seeking more preferred foods. If that is the case it may be more correct for future studies to focus on 'lean' seasons rather than years.

In both 2005 and 2006, female and male diet in the dry season were not significantly different. This may be due to increased overall food availability in these years compared to 2013-2014, resulting in less competition and both sexes eating a diet closer to 'optimal'. In 2005, however, female dry season diet was also not significantly different from males in the wet season, whereas female diet in the wet season was. This creates the odd situation where male wet season diet was more similar to females' diet in the opposite season than the concurrent. It is possible that the explanation lies in the increase in food availability during the wet season; because increase in total availability was still less that than the dry season, and there was not an increase in fruit availability. As a result potentially the more competitive males were able to better exploit and monopolise the resources, as a result making their diet more similar to the dry season. The less competitive females potentially could not do this and therefore kept a more typical wet season diet. A better understanding of which species *C. nictitans* prefer may help clarify the cause of this interesting pattern.

Variation due to troop membership

There was significant difference in the diet of the two troops observed in 2013-2014. The smaller troop, MFT, was more folivourous than the larger BBT. This increase was due only to increased consumption of less favourable old leaves, and MFT ate half as many new leaves and less of all non-leaf food types. This probably reflects between -group intra-specific competition for food types (Whitten 1988). BBT was notably larger than MFT and the troops had a notable degree of home range overlap, as such it is likely they competed for the same food resources and as BBT had a competitive advantage they consumed a greater proportion of preferred foods. This fits with predictions that size of the troop will impact the relative proportion of foods in the diet (Hare 2001, Porter et al. 2014). In turn highlighting the risk of generalising diet and also of making conservation decisions based on observations of only one troop. This is especially true if, unlike these two troops, there is large variation in the food species composition or availability in their home range.

Factors influencing diet

Though differences were present between female and male *C. nictitans* diet, they were found to be less important in explaining diet than factors relating to availability. The factors found to significantly influence proportional consumption were *year*, *season*, *food type*, and the interactions of *season and food type* and *year and food type*. As with earlier analyses, 2013-2014 was found to be different from other years, with this difference largely due to the observed increased arthropod consumption. Season was also important due to the increase in arthropod consumption in the wet season. The consumption of 'other' food types in 2006 was significant, during this period consumption was over twice as high as other years. However without monitoring availability it is not possible to determine why this may be. The fact that 'other' is an amalgamation of a number of highly varied foods, some consistently available and others transient, further complicates the matter. *Arthropod* and *'other'* also had significant independent effects, along with the fruit and leaves. Like other primates (Gautier-Hion 1980, Kaplin and Moermond 2000, Brugiere et al. 2002, Kaplin and Lambert 2002, Chapman and Russo 2007), *C. nictitans* appears to maximise fruit consumptions whenever it can, with the only variation occurring during the period of extreme scarcity during the 2013-2014 wet season. Leaves were consistently present in the diet, and along with arthropods, appear to undergo increased consumption during periods of scarcity. Again the exception being males during the 2013-2014 wet season.

Better understanding availability and nutritional value would help us better understand *C. nictitans* diet, and why there was such a swing to arthropod consumption during that period.

Conclusion

During the study the diet of *C. nictitans* varied in response to a number of factors related to scarcity. This response ranged from a diet made up of three quarters fruit to three quarters arthropods. For *C. nictitans*, as for many other primates, it is an increasingly stressful world with an ever increasing human population resulting in diminishing and increasingly fragmented habitat with less variable and less available food resources. Though *C. nictitans* appears to prefer fruit when available, in this study it appeared to demonstrate dietary flexibility typical of Cercopithinae suggesting they too should be able to persist in degraded habitats. Further study is required to determine if this behaviour is typical of all 'lean' years, and whether or not it is applicable to *C. nictitans* in other forests or habitats. Though *C. nictatns* appears to consume a variety of fruit species, it is yet to be determined how effective seed dispersal is across both 'average' and 'lean' years, how much overlap there is in seed dispersal by *C. nictitans* with other species at NMFP. However the variety of seed species consumed, and the novel finding of consumption of the large seeded *Cordia millenii suggests that at least for NMFP, C. nictitans may play a role partially offsetting the loss of other large bodied dispersers. To better understand observed variation in diet future studies should include a greater number of male C. nictitans. Specifically, non-troop models to determine if their diet or habitat use is significantly different from troop-males, if this is the case it may be a source of notable skew in current result. Future studies, where possible, should also include nutrient analysis of food items, to help understand why C. nictitans* utilises different foods during different levels of scarcity.

References

Albert, A., K. McConkey, T. Savini, and M.-C. Huynen. 2014. The value of disturbance-tolerant cercopithecine monkeys as seed dispersers in degraded habitats. Biological Conservation **170**:300-310.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour **49**:227-266.

Arnold, K., and K. Zuberbühler. 2008. Meaningful call combinations in a non-human primate. Current Biology **18**:doi:10.1016/j.cub.2008.1001.1040.

Babweteera, F. 2009. *Cordia millenii*: on the risk of local extinction? African Journal of Ecology **47**:367-373.

Basabose, A. K. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American journal of primatology **58**:1-21.

Basabose, A. K. 2004. Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. Primates **45**:211-219.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological):289-300.

Benjamini, Y., and D. Yekutieli. 2001. The control of the false discovery rate in multiple testing under dependency. Annals of statistics:1165-1188.

Blaser, J. 2011. Status of tropical forest management 2011. International Tropical Timber Organization.

Bond, W. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society B: Biological Sciences **344**:83-90.

Borokini, T., F. Babalola, T. Amusa, S. Ivande, Z. Wala, O. Jegede, D. Tanko, and J. Ihuma. 2012. Community-based Forest Resources Management in Nigeria: Case study of Ngel Nyaki Forest Reserve, Mambilla Plateau, Taraba State, Nigeria. Journal of Tropical Forestry and Environment **2**:69-76.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, and G. Magin. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation biology **16**:909-923.

Brugiere, D., J.-P. Gautier, A. Moungazi, and A. Gautier-Hion. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology **23**:999-1024.

Butynski, T. M. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-and low-density subpopulations. Ecological Monographs:1-26.

Butynski, T. M. 2002. The guenons: Diversity and adaptation in African monkeys. Kluwer Academic, New York.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Chapman, C. 1987. Flexibility in diets of three species of Costa Rican primates. Folia Primatologica **49**:90-105.

Chapman, C. A., and L. J. Chapman. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates **40**:215-231.

Chapman, C. A., L. J. Chapman, M. Cords, J. M. Gathua, A. Gautier-Hion, J. E. Lambert, K. Rode, C. E. Tutin, and L. J. White. 2002. Variation in the diets of Cercopithecus species: differences within forests, among forests, and across species. Pages 325-350 The guenons: Diversity and adaptation in African monkeys. Springer.

Chapman, C. A., L. J. Chapman, L. Kaufman, and A. E. Zanne. 1999. Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. African Journal of Ecology **37**:81-92.

Chapman, C. A., and D. A. Onderdonk. 1998. Forests without primates: primate/plant codependency. American journal of primatology **45**:127-141.

Chapman, C. A., and S. E. Russo. 2007. Primate seed dispersal. Primates in perspective. New York: Oxford University Press:510-525.

Chapman, H. M., S. L. Goldson, and J. Beck. 2010. Postdispersal removal and germination of seed dispersed by Cercopithecus nictitans in a West African montane forest. Folia Primatologica **81**:41-50.

Chapman, H. M., S. M. Olson, and D. Trumm. 2004. An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. Oryx **38**:282-290.

Chapman, J., and H. Chapman. 2001. The Forests of Taraba and Adamawa States, Nigeria. *An Ecological Account and Plant Species Checklist*. University of Canterbury, New Zealand.

Clout, M., and J. Hay. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand journal of ecology **12**:27-33.

Clutton-Brock, T., and P. Harvey. 1977. Species differences in feeding and ranging behaviour in primates. In (T. Clutton-Brock, Ed.) Primate Ecology. London: Academic Press.
Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences 100:14052-14056.
Cords, M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. The Journal of Animal Ecology 55:811-827.
Cramer, J. M., R. C. Mesquita, and G. B. Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation 137:415-423.
Cristobal-Azkarate, J., and V. Arroyo-Rodriguez. 2007. Diet and activity pattern of howler monkeys (Alouatta palliata) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. American journal of primatology 69:1013.
Cunningham, S. A. 2000. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society of London B: Biological Sciences 267:1149-1152.
Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. Murray, London, U.K.
Dirzo, R., and P. H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137-167.
Duncan, R. S., and C. A. Chapman. 2002. Limitations of Animal Seed Dispersal for Enhancing Forest Succession on Degraded Lands. Pages 437-450 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing., Wallingford, U.K.
Dutton, P., and H. Chapman. 2015. Dietary preferences of a submontane population of the rare Nigerian-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Ngel Nyaki Forest Reserve, Nigeria. American journal of primatology 77:86-97.
Eckardt, W., and K. Zuberbühler. 2004. Cooperation and competition in two forest monkeys. Behavioral Ecology 15:400-411.
Fa, J. E., J. Juste, J. P. Val, and J. Castroviejo. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conservation biology 9:1107-1115.
Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics 34:487-515.
Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. Conservation biology 19:680-688.
Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, W. J. Foley, J. T. Wood, I. R. Wallis, and D. B. Lindenmayer. 2009a. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology:doi: 10.1093/beheco/arp1021.
Felton, A. M., A. Felton, J. T. Wood, W. J. Foley, D. Raubenheimer, I. R. Wallis, and D. B. Lindenmayer. 2009b. Nutritional ecology of Ateles chamek in lowland Bolivia: how macronutrient balancing influences food choices. International Journal of Primatology 30:675-696.
Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, and H. K. Gibbs. 2005. Global consequences of land use. Science 309:570-574.
Food, and A. O. o. t. U. Nations. 2010. Global forest resources assessment 2010: Main report. Food and Agriculture Organization of the United Nations.
Galetti, M., R. Laps, and M. A. Pizo. 2000. Frugivory by Toucans (Ramphastidae) at Two Altitudes in the Atlantic Forest of Brazil 1. Biotropica 32:842-850.
Ganas, J., and M. M. Robbins. 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. Behavioral Ecology and Sociobiology 58:277-288.
Garber, P. 1987. Foraging strategies among living primates. Annual review of Anthropology 16:339-364.
Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. The Journal of Animal Ecology 49:237-269.
Gautier-Hion, A. 1988. The diet and dietary habits of forest guenons. Pages 257-283 A primate radiation: Evolutionary biology of the African guenons. Cambridge University Press, Cambridge.
Gautier-Hion, A., J.-P. Gautier, and R. Quris. 1981. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). Revue D Ecologie-La Terre Et La Vie 35:512-536.

Gautier-Hion, A., R. Quris, and J.-P. Gautier. 1983. Monospecific vs polyspecific life: a comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. Behavioral Ecology and Sociobiology 12:325-335.
Gawaisa, S. 2006. How important are putty nosed monkeys (*Cercopithecus nicitans*) in montane forest seed dispersal? Federal University of Technology.
Gross-Camp, N. D., and B. A. Kaplin. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. Acta Oecologica 37:578-586.
Gupta, A., and D. J. Chivers. 1999. Biomass and use of resources in south and south-east Asian primate communities. Pages 38-54 Primate Communities. Cambridge University Press, Cambridge.
Hand, D. J., and C. C. Taylor. 1987. Multivariate analysis of variance and repeated measures: a practical approach for behavioural scientists. Chapman & Hall, London.
Hanski, I. 2005. Landscape fragmentation, biodiversity loss and the societal response. EMBO reports 6:388-392.
Hanya, G., N. Noma, and N. Agetsuma. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. Primates 44:51-59.
Happel, R. 1988. Seed-eating by West African cercopithecines, with reference to the possible evolution of bilophodont molars. American Journal of Physical Anthropology 75:303-327.
Hare, B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? Animal cognition 4:269-280.
Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493-495.
Harrison, M. J. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Animal behaviour 31:969-977.
Hill, C. M., and A. D. Webber. 2010. Perceptions of nonhuman primates in human–wildlife conflict scenarios. American journal of primatology 72:919-924.
Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. BioScience 54:651-660.
Irwin, M. T., J.-L. Raharison, D. R. Raubenheimer, C. A. Chapman, and J. M. Rothman. 2015. The Nutritional Geometry of Resource Scarcity: Effects of Lean Seasons and Habitat Disturbance on Nutrient Intakes and Balancing in Wild Sifakas. PloS one 10:DOI:10.1371/journal.pone.0128046.
Jones, C. 1980. The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous neotropical primate. Primates 21:389-405.
Jones, M. E., and L. A. Barmuta. 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. Journal of animal ecology 67:410-421.
Kaplin, B., and T. Moermond. 2000. Foraging ecology of the mountain monkey (*Cercopithecus l'hoesti*): implications for its evolutionary history and use of disturbed forest. American journal of primatology 50:227-246.
Kaplin, B., V. Munyaligoga, and T. Moermond. 1998. The Influence of Temporal Changes in Fruit Availability on Diet Composition and Seed Handling in Blue Monkeys (*Cercopithecus mitis doggetti*). Biotropica 30:56-71.
Kaplin, B. A., and J. E. Lambert. 2002. Effectiveness of Seed Dispersal by Cercopithecus Monkeys: Implications for Seed Input into Degraded Areas.*in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, New York.
Kaplin, B. A., and A. William. 2013. Behavior within groups.*in* E. Sterling, N. Bynum, and M. Blair, editors. Primate Ecology and Conservation. Oxford University Press, Oxford.
Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, and J. Pino. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology letters 13:597-605.
Lawes, M. 1991. Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in the Cape Vidal dune forest, South Africa. Journal of Zoology 224:149-173.
Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22-30.
Marshall, A. J., C. M. Boyko, K. L. Feilen, R. H. Boyko, and M. Leighton. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614.
Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology 28:1219-1235.
Martin, P., and P. Bateson. 1986. Measuring behavior. Cambridge Univ. Press, Cambridge.
McConkey, K. R., and W. Y. Brockelman. 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology 92:1492-1502.

McConkey, K. R., and D. R. Drake. 2006. Flying foxes cease to function as seed dispersers long before they become rare. Ecology 87:271-276.
McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biological Conservation 146:1-13.
Mitani, M. 1991. Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. Primates 32:137-151.
Moberg, F., and P. Rönnbäck. 2003. Ecosystem services of the tropical seascape: interactions, substitutions and restoration. Ocean & Coastal Management 46:27-46.
Moran, C., C. Catterall, R. J. Green, and M. F. Olsen. 2004. Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. Oecologia 141:584-595.
Nilsen, E. T., and D. M. Orcutt. 1996. Abiotic factors.
Nishida, T. 2002. Competition between baboons and chimpanzees at Mahale. Pan Afrrican News 9:23-26.
O'Brien, R. G., and M. K. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. Psychological bulletin 97:316.
O'Driscoll Worman, C., and C. A. Chapman. 2005. Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. Journal of Tropical Ecology 21:689-697.
Oates, J. F., and C. P. Groves. 2008. *Cercopithecus nictitans*.
Onderdonk, D. A., and C. A. Chapman. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. International Journal of Primatology 21:587-611.
Parrotta, J. A., J. W. Turnbull, and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:1-7.
Pimm, S. L., and P. Raven. 2000. Biodiversity: extinction by numbers. Nature 403:843-845.
Porter, L. M., C. C. Gilbert, and J. G. Fleagle. 2014. Diet and phylogeny in primate communities. International Journal of Primatology 35:1144-1163.
Poulsen, J. R., C. J. Clark, E. F. Connor, and T. B. Smith. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. Ecology 83:228-240.
Robinson, J. G. 1984. Diurnal variation in foraging and diet in the wedge-capped capuchin *Cebus olivaceus*. Folia Primatologica 43:216-228.
Rothman, J. M., C. A. Chapman, and P. J. Van Soest. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542-566.
Rowell, T. E., and B. J. Mitchell. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. Journal of Tropical Ecology 7:269-274.
Ruxton, G. D., and H. M. Schaefer. 2012. The conservation physiology of seed dispersal. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1708-1718.
Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333-353.
Setchell, J. M., and D. J. Curtis. 2011. Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge.
Sorensen, T. C., and L. M. Fedigan. 2000. Distribution of three monkey species along a gradient of regenerating tropical dry forest. Biological Conservation 92:227-240.
Stoner, K. E., P. Riba-Hernández, K. Vulinec, and J. E. Lambert. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica 39:316-327.
Struhsaker, T. T. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Florida.
Thia, J. A. 2014. The plight of trees in disturbed forest: conservation of Montane Trees, Nigeria.
Tsujino, R., and T. Yumoto. 2009. Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. Journal of animal ecology 78:119-125.
Tutin, C., R. Ham, and L. White. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American journal of primatology 42:1-24.
Tutin, C., and L. White. 1998. Primates, phenology and frugivory: Present, Past and Future Patterns in the Lopé Reserve, Gabon. Page 309 *in* Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society. Cambridge University Press.
Tutin, C. E. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249-265.

Vieira, D. L., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. Restoration Ecology **14**:11-20.
Vitousek, P. M., and R. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual review of ecology and systematics **17**:137-167.
Waterman, P. G., G. M. Choo, A. L. Vedder, and D. Watts. 1983. Digestibility, digestion-inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. Oecologia **60**:244-249.
Whitten, P. 1988. Effects of patch quality and feeding subgroup size on feeding success in vervet monkeys (*Cercopithecus aethiop*s). Behaviour **105**:35-52.
Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American naturalist **125**:879-887.
Williams-Linera, G. 1997. Phenology of deciduous and broadleaved-evergreen tree species in a Mexican tropical lower montane forest. Global Ecology and Biogeography Letters:115-127.
Winterhalder, B. 1981. Optimal foraging strategies and hunter-gatherer research in anthropology: theory and models. Pages 13-35 *in* B. Winterhalder and A. E. Smith, editors. Hunter-gatherer foraging strategies: Ethnographic and archaeological analyses. University of Chicago Press, Illinois.
Wrangham, R. W., C. A. Chapman, and L. J. Chapman. 1994. Seed dispersal by forest chimpanzees in Uganda. Journal of Tropical Ecology **10**:355-368.
Wrangham, R. W., N. L. Conklin-Brittain, and K. D. Hunt. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. . International Journal of Primatology **19**:949-970.
Wunderle Jr, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**:223-235.
Yumoto, T., N. Noma, and T. Maruhashi. 1998. Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates **39**:325-338.
Zar, J. H. 1999. Biostatistical analysis. Pearson Education, India.
Zuidema, P. A., J. A. Sayer, and W. Dijkman. 1996. Forest fragmentation and biodiversity: the case for intermediate-sized conservation areas. Environmental conservation **23**:290-297.

3 |Do *Cercopithecus nictitans* consume large fruited species and could they be an effective large seed disperser at Ngel Nyaki Forest Reserve?

Introduction

Seed dispersal is one of the most important mutualisms on the planet (Lambert 2010). However it is increasingly put at risk through processes such as habitat loss and fragmentation (Zuidema et al. 1996, Dirzo and Raven 2003, Fahrig 2003, Hanski 2005, Krauss et al. 2010). In tropical forest systems up to 90 percent of trees and shrubs produce fleshy fruit adapted for animal dispersal (Chapman et al. 2010, McConkey et al. 2012). Loss or degradation of habitat on which these animals depend, can result in a loss or decrease in wildlife. Loss of wildlife has been shown to lead to changes in fruit dispersal patterns and a subsequent change in community composition within a forest ecosystem (Chapman et al. 2010, McConkey et al. 2012), potentially disrupting the ecosystem services that they provide (Duncan and Chapman 2002, Fearnside 2005, Foley et al. 2005).

Large bodied animal species in particular have a high extinction risk due to both intrinsic and environmental factors; they tend to live at lower population densities, have a lower intrinsic rate of population increase, and be subject to higher hunting pressure (Wilcox and Murphy 1985, Cardillo et al. 2005). Loss of these species can have particularly devastating effects on a forest community. Firstly, as large bodied species can have a disproportionately large impact on their ecosystem. For example, Wrangham et al. (1994) found that despite only comprising 1.4% of the primate frugivore population and 14.2% of primate frugivore biomass, *Pan troglodytes* (common chimpanzee) accounted for around 45.3% of seeds defecated by frugivorous primates. Secondly, as typically in tropical forests as fruit and seed size increases there is a corresponding decrease in dispersers. This is because smaller species lack the gape to consume and disperse large seeds (Wheelwright 1985, Chapman et al. 1992, Peres and van Roosmalen 2002, Chapman et al. 2010).

Primates serve as an important disperser of medium and large seeds in tropical forests, having been shown to be responsible for as much of 74% of all fruit removal in a forest (Chapman and Onderdonk 1998). Effiom et al. (2013)

demonstrated the impact the loss of primates can have on forest communities. They showed that forests in Nigeria with impoverished primate communities had lower recruitment of animal-dispersed trees and higher recruitment of abiotically-dispersed trees compared to protected forests. Like other large bodied species however, many primate dispersers are at risk of local or global extinction with larger relative body size being associated with greater risk (Purvis et al. 2000, Matthews et al. 2010).

Surrogate dispersal

The loss of large bodied primate disperser may be able to be minimised or offset by 'surrogate dispersers' (Albert et al. 2014). The introduction of such surrogate species or support via targeted conservation efforts of more resilient species already present, has been proposed as a means to encourage habitat regeneration. Species choice however needs to be done with careful consideration of functional roles, to avoid the introduction of pest species that will further burden on the system. Species need to be both capable of effectively dispersing medium and large seeds that may otherwise face a dispersal crisis; whilst also being resilient to anthropogenic disturbance.

Cercopithecine monkeys have been identified as potentially important species in degraded habitats and are potential candidates for filling surrogate disperser roles in Asian and African habitats (Chapman et al. 2010, Albert et al. 2014). Cercopithecine species are unique amongst primates for possessing large cheek pouches (Butynski 2002). These can store nearly as much as the monkeys stomach and are associated with seed spitting as a means of dispersal (Chapman and Russo 2007). Spitting allows Cercopithecinae to disperse both a greater quantity and larger seeds than it could via swallowing (Lambert 2001, Albert et al. 2014). Furthermore, due to a high level of ecological flexibility nearly 80% of Cercopithecinae are able persist in disturbed habitats (Albert et al. 2014). This disturbance tolerance, the possession of cheek pouches, a typically large home range, omnivorous diet and tendency towards semi-terrestriality have all been proposed as factors that may make cercopithecinae highly valuable seed dispersers in degraded habitats (Albert, McConkey et al. 2014). Cercopithecine monkey's disturbance tolerance however has led many to consider them pests. Due to this they have been largely understudied (Hey 1964, King and Lee 1987, Else 1991, Albert et al. 2014). As a result it is not clear for some species which fruit species they consume and potentially disperse, or if they do this effectively. It is pertinent that this is determined before any species is considered for a surrogate role.

Chapman et al. (2010) proposed that in Ngel Nyaki Forest Reserve (NMFP), an Afromontane forest in Nigeria, *Cercopithecus nictitans* (putty-nosed monkey) may be a 'surrogate disperser', partially offsetting the loss of the

previously common *Pan troglodytes ellioti* (Nigerian/Cameroon chimpanzee). The severe reduction in *P. t. elotti* biomass and the extinction of *Loxodonta Africana* (African bush elephant) means that large fruited species at NMFP may be undergoing a seed dispersal crisis, having nearly lost two of the small set of dispersers with large enough gapes to consume them (Borokini et al. 2012, Thia 2014). Chapman et al. (2010) found that *C. nictitans* at NMFP defecated seeds with a mean length of up to 24.7mm, comparable to findings in the same forest by Dutton and Chapman (2015) for *P. t. ellioti* where the largest seed species found in faecal matter had a mean length of 28.5mm. Seeds were widely dispersed by *C. nictitans,* with defecated seeds showing enhanced germination rates in three species tested. The length of the study however meant that only a small snapshot of *C. nictitans* diet was captured, it is therefore unknown how many species with medium or large seeds they may potentially disperse or if the consume these species with any consistency (Marshall and Wrangham 2007).

To gain a better understanding of *C. nictitans* potential as a surrogate disperser in disturbed Nigerian Montane forest, I investigated their potential effectiveness as a seed disperser with a focus on whether they showed positive selection for large fruit species or those with medium or large seeds that may otherwise face a dispersal crisis. In previous work (Chapter 2), I determined the species that constituted *C. nictitans* diet within this habitat and demonstrated that diet was flexible changing with food availability. To build upon this I investigated potential indicators of effective seed dispersal by *C. nictitans* living in NMFP. Schupp (1993) stated seed dispersal effectiveness was best measured as the 'number of new adults produced by the dispersal activities of a disperser'. This is however both time consuming and costly (Schupp et al. 2010). Investigating instead if *C. nictitans* possessed expected characteristic of an effective disperser, allowed a cost effective means which could utilise existing data to determine areas or species on which to focus future research. For instance, is *C. nictitans* was found to not consume large fruited species, it would not be fiscally frugal to continue to investigate it as a potential surrogate disperser for *P. t. ellioti*,

To investigate potential effectiveness of *C. nictitans* as a seed disperser I compared the overlap of diet between years, seasons and sexes; changes in niche width with year, seasons and sex; and variation in diet with time of day. To investigate how effectively they may disperse species with medium and large seeds I looked at relative consumption compared to other species in each year and season; preference for species in each year and season by female and male *C. nictitans;* pretence for fruit of species in each year; and whether *C. nictitans* showed positive selection for large seed characteristics.

C. nictitans as a seed disperser

Dietary overlap

Dietary overlap is the amount of shared food items in the diet of two consumers of interest (Schoener 1968). Comparing overlap in diet between years shows what proportion of food items are shared between years with differing availability (Mysterud 2000, Elmhagen et al. 2002, Phillips et al. 2007). As disperser reliability has a temporal component, in part depending on how often trees are visited, comparing overlap between years can inform us to disperser effectiveness (Kaplin and Lambert 2002). Consistency in seed dispersal, and thus greater effectiveness, would be indicated by a large overlap in diet between years.

Great flexibility has been observed in primate diets, with changes in dietary strategy (e.g. frugivorous, foliovorous) from one month to the next (Chapman 1987, Gautier-Hion 1988, Tutin, Ham et al. 1997). Cercopithecines are no exception, being characterised by ecological flexibility including adjustments in diet (Gautier-Hion 1988, Tutin, Ham et al. 1997, Albert, McConkey et al. 2014). Though this flexibility helps Cercopithecines persist in disturbed habitats, however it also has direct consequences on seed dispersal reliability (Albert, McConkey et al. 2014).

I compared overlap in diet of *C. nictitans* between years of low, medium and high food availability as previous work at NMFP forest indicated that *C. nicitians* diet was highly flexible, with in dietary strategy in response to low food availability (see Chapter 2). Previous work indicated a marked effect of seasonal availability in *C. nictitans* at NMFP, so I also compared overlap between wet and dry seasons. I predicted that due to the flexibility in their diet there would be little overlap in *C. nictitans* diet between periods of high and low availability.

Reduced food abundance has also been linked to increased intra-specific competition within group competition (Cords 1986). This increased competition can result in portioning of resources or broadening of dietary niche, both of which decrease observed overlap (Schoener 1970, Gautier-Hion 1980, Yeager 1989, Kaplin, Munyaligoga et al. 1998, Kaplin and Moermond 2000, Stevenson, Quiñones et al. 2000). Therefore overlap within a group should be lowest when competition is highest, which has been observed in studies of Cercopithecus species (Chapman, Chapman et al. 2002). Contrary to this prediction however, Lawes, Henzi et al. (1990) found greater similarity in *C. mitis* in the dry season, as the marked decrease in food meant that there was less choice leading to high similarity in diet.

In previous work it was found that during the 'lean' year female and male *C. nictitans* had significant differences in proportions of food types consumed, not present during times of higher availability. It therefore seems

unlikely that their diet became more similar as seen in Lawes, Henzi et al. (1990) . Subsequently I predicted I would see a decrease in overlap between female and male *C. nictitans* diets in periods of lower availability.

Niche Width

Primates do not eat all potential foods available in a forest, instead they select a subset. This subset is their dietary niche and its width indicates how selective or generalist a species is (Shipley, Forbey et al. 2009). Niche width varies with availability. When preferred foods (foods eaten disproportionately more than their availability), such as fleshy fruits, are abundant the niche should be narrow as primates focus on utilising these food types (Irwin, Raharison et al. 2015). When preferred foods are scarce the niche should increase as primates branch out and utilise less preferred food types (Chapman et al. 2002)..

This pattern has been observed in *C. mitis doggetti* (Doggett's blue monkey) in tropical montane forests in Rwanda, where in response to scarcity animals employed different strategies including the increased consumption of leaves and less preferred fleshy fruit, and becoming seed predators (Kaplin, Munyaligoga et al. 1998).

In NMFP *C. nictitans* was observed to switch diet strategy in response to availability. Furthermore though they consumed a total of 32 species they did not consume all these species in any one year (see Chapter 2). With significant differences in diet in the 'lean' year compared to those with higher availability. As such it appears they are altering their diet in response to availability and therefore I predicted that there would be significant differences in niche width, with less species consumed in periods of high availability.

Not all strategies are equal, and which foods are used during times of scarcity have variable quality, as with food items at any time of year (Chapman et al. 2002). When food is scarce there may not be enough for all individuals to switch to the same alternate strategy (Kaplin et al. 1998b). Less competitive individuals may need to employ a number of comparatively less effective strategies, resulting in a wider width than better competitors (Harrison 1983).

As males are larger they tend to have first choice of resources, this means if the capacity to utilise a strategy is limited males are most likely to utilise the most effective strategy and have a narrow niche width. I therefore predicted that male *C. nictitans'* niche width would be narrower than females and that it would increase less during periods of scarcity.

Variation with time of day

The time of day that fruit is consumed may impact on a species ability to act as a seed disperser due to variation in activity pattern (Clutton-Brock and Harvey 1977, Gautier-Hion 1980, Robinson 1984, Kinnaird et al. 1999). A seed consumed in the morning is, depending on gut passage time, more likely to be defecated while troops are moving, whereas seed consumed in the afternoon is more likely to be defecated at night i.e. while troops are resting, resulting in less variable seed dispersal (Chapman and Russo 2007).

Primate diets may vary in response to varying energy requirements throughout the day (Clutton-Brock and Harvey 1977, Gautier-Hion 1980, Robinson 1984, Kinnaird et al. 1999). Not all food types are equal, fruits provide an easy source of carbohydrates and thus quick energy but are a poor source of protein, arthropods are rich in readily available protein but are active only at certain times of day and in some species with time of year, new leaves and flowers are also a source of protein however they are less readily available, they are also a less available source of energy than fruits (Lawes 1991). This may result in different food types being most suitable for an animal's needs at different times of day (Clutton-Brock and Harvey 1977, Gautier-Hion 1980, Robinson 1984).

Previous studies found a reliable pattern of morning and/or afternoon fruit consumption in most primate species (Clutton-Brock and Harvey 1977, Gautier-Hion 1980, Robinson 1984, Kinnaird et al. 1999). It was proposed that this provides primates with the energy needed for the day after a period of rest or zero-energy intake, or gives them the food they require before the evening fast (Chapman and Chapman 1991). Leaves are typically consumed in the afternoon, potentially as the lower energy requirements of rest limit the disadvantages of slow digestion of leaves. Arthropods are usually consumed when they are active which is typically around midday (Clutton-Brock and Harvey 1977, Gautier-Hion 1980). A recent case study found that *P. troglodytes* fed on leaves in the late afternoon when their quality was highest, tracking nutrient composition over short time periods (Carlson et al. 2013). This may also help explain the tendency towards afternoon consumption of leaves seen in other primate species.

Due to the consistency of previous patterns I predicted I would observe a higher proportion of independent feeding observations of fruit in the morning and afternoon compared to other food types and that the proportion of leaves consumed would increase as the day progressed.

C. nictitans as a large seed disperser

Ranks

To be an effective seed disperser a species must consume an appreciable amount of a fruit species (Howe and Smallwood 1982). Thought the exact amount varies depending on plant life strategy, it is unlikely that a disperser species that eats only one fruit a year of a large seed plant will have any notable effect (Schupp et al. 2010). Species which make up a larger proportion of a disperser's diet are more likely to be effectively dispersed (Howe and Smallwood 1982, Schupp et al. 2010). However as dispersal also has a temporal component, this is only true if they are eaten in large quantities reliably over time (Kaplin and Lambert 2002).

Due to large seeds having been previously found in moderate quantities in *C. nictitans* faeces I predicted that they were consuming appreciable amounts of some medium and large seeded species. However due to aforementioned flexibility in diet I predicted that they were not doing this reliably over time.

Male and female primates have different life histories and as such they have different dietary requirements (Gautier-Hion 1980, Harrison 1983). Males tend to utilise more readily accessible energy sources, such as fruit, allowing them to more easily perform vigilance tasks. Females, especially pregnant and lactating females, tend to have higher consumption of new leaves and arthropods due to the high protein content (Gautier-Hion 1980, Harrison 1983). As mentioned previously, sexual dimorphism also means males tend to have greater access to preferred resources compared to females (Gautier-Hion 1980, Porter et al. 2014).

Therefore I predicted that if *C. nictitans* showed preference for medium and large seeded species they would be differentially consumed by the different sexes.

Preference

The amount of a particular food in a consumer's diet depends on the availability of the food as well as the consumer's electivity or preference for the food (Poulsen, Clark et al. 2002). Preference can also impact on a species reliability as a seed disperser on both a spatial and temporal scale as they are more likely to visit all individuals of a preferred species and as they are more likely to visit consistently through time (Kaplin and Lambert 2002). Previous work has shown that primates, including *C. nictitans*, tend to show preference for large fleshy fruit (Gautier-Hion 1980, Kaplin and Moermond 2000, Brugiere et al. 2002, Kaplin and Lambert 2002, Chapman and Russo 2007), however preference has

been shown to vary with age, sex, forest composition and abundances, and supra-annual fruiting phenologies (Stevenson 2004, Russo, Campbell et al. 2005).

I hypothesised that *C. nictitans* would show preference for a number of large fleshy fruit species but would show varying preference in 'lean' years compared to 'normal' and 'high' years. Furthermore that as intraspecific competition is predicted to result in niche portioning, that males and females will show different preferences within years and seasons (Schoener 1970, Gautier-Hion 1980, Yeager 1989, Kaplin, Munyaligoga et al. 1998, Kaplin and Moermond 2000, Stevenson, Quiñones et al. 2000). As scarcity in 2013-2014 was related to a decrease in mature fruit availability, I predicted that there would be less large fruit preferred in 2013-2014 due to a lack of availability.

Selection for seed size

Seeds can vary in a number of characteristics including size, weight, number and shape (Tripathi and Khan 1990). These impact on how easy they are to process, swallow and defecate (Henrik Bruun and Poschlod 2006, Forget et al. 2007). Though *C. nictitans* can spit seeds they also disperse seeds via swallowing (Butynski 2002). Seeds that are easy to swallow and defecate tend to be 'pill' shaped and small (Gross-Camp and Kaplin 2005, Vander Wall et al. 2005). Due to plant life strategies small seeds also tend to be numerous (Taylor et al. 1990). If seeds are passed whole they do not provide nutritional benefit, or 'reward'. To limit time feeding primates tend to consume large fleshy fruits, to maximise energy intake (Gautier-Hion et al. 1985, Chapman 1995).

As such I predicted that *C. nictitans* would favour species with seeds which are easier to swallow. These would be small, numerous, oval and found with a large amount of fruit flesh. I also predicted that they would prefer these in all years.

Methods

Study Site

My study was conducted at NMFP, a submontane forest reserve located on the western escarpment of the Mambilla Plateau (7°30 N, 11°30 E), in Taraba State. Further details on site characteristics can be found in Chapter 2.

Subjects and behavioural observations

Behavioural observations were conducted over three years, on three different *C. nictitans* troops. The first troop, SGT, was observed between January 2005 and December 2006 and the remaining two troops, BBT and MFT, were observed concurrently between November 2013 and October 2014 inclusive. Troops were followed from dawn to dusk and observations were conducted using scan sampling (Altmann 1974). During scans species and 'type' of food items consumed were recorded. Type was selected from one of six categories: fruit, new leaves, old leaves, flowers, arthropods or 'other'. Further details on observation methods and troop demographics can be found in Chapter 2.

Characterisation of years

Previous work characterised the years of observation in terms of food availability. Food availability was defined as abundance of flowers, fruit and leaves in all stages of maturity along established phenology transects. An analogue of abundance was calculated based on percentage coverage and the basal area of the tree.

Average monthly food availability was calculated using data from 2005-2013 and compared with each of the years. It was found that food availability in 2006 was not significantly different from average. In 2005 it was different, being slightly higher than average. In 2013-2014 there was significantly less food available than average overall and less fruit available in every month except September. The difference in availability was found to be more extreme for species in *C. nictitans* diet compared to overall (see Chapter 2).

In all years both female and male diet was significantly different between the wet and dry season. Typically, during the dry season *C. nictitans* consumed more flowers, fruit and 'other' food types. This was mirrored in greater availability of flowers and fruits, as well as greater total food availability during the dry season.

Fruit Characteristics

To investigate whether *C.* nictitans showed preference for certain seed characteristics, 24 fruit species were characterised by a visiting student, Umar Lawrence, with the assistance of local field assistants. This work

was conducted between November 2014 and June 2015. Lawrence was trained remotely with the assistance of the field station's science co-ordinator. To ensure the accuracy of his work photos were taken of collected fruit, as well as of measurements of fruit and seeds using callipers. His work was also observed by my primary supervisor, Hazel Chapman, during a visit to the field station.

For each species, 20 ripe fruit were collected and measured. Where possible this was five fruit from four trees, though this was not always achieved no species had all its fruit collected off one tree. From these fruit a total of 20 seeds were randomly selected for measurement. Species chosen for collection were determined by presence in *C. nictitans* diet, aiming to get a range from common to complete absence, as well as by fruiting availability during the collection period. Seed characteristics measured were seed number, weight, length, width and height. From measurements the ratio of seed width to length were calculated to give an indication of how elongate the seed was. Fruit length, width and height were also used to calculate seed volume to fruit volume ratio. This was determined as follows:

1)

$$\mathrm{F{:}S} = \frac{\mathrm{N}(\mathrm{V_S})}{\mathrm{V_F}}$$

Where:

$$\mathrm{F{:}S} = \text{Propotion seed size contributes to total fruit size}$$

$$\mathrm{N} = \text{Average number of seeds for a given species}$$

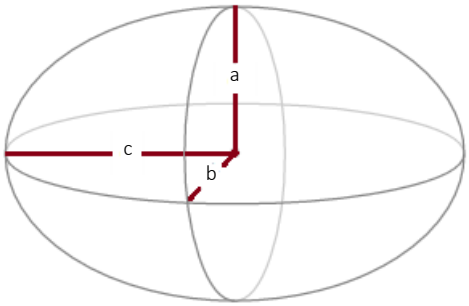
$$\mathrm{V_S} = \text{Volume of seed}$$

$$\mathrm{V_F} = \text{Volume of fruit}$$

2)

$$\mathrm{V} = \frac{4}{3}\pi\mathrm{abc}$$

Where:



C. nictitans as a seed disperser

Calculations for selectivity, overlap and preference were calculated by hand in Microsoft Excel.

Overlap

To calculate dietary similarity between sexes and years I used Schoener's index of niche overlap (R_o) (Schoener 1970). The index ranges from 0 (no overlap) to 1 (complete overlap). It is calculated as:

$$R_o = 1.0 - 0.5 \left(\sum |p_{x,i} - p_{y,i}| \right)$$

Where

$R_o =$ Index of overlap

$P_{x,i} =$ Proportion of plant species in diet of group x

$P_{y,i} =$ Proportion of plant species in diet of group y

So that the analysed percentages were of the plant diet only, I summed plant parts into three categories for each species (flower, fruit and leaves) and, as insects were excluded, scaled these to 100% before calculating proportions. I then calculated overlap between female and male *C. nictitans* diet both overall and within each year, to investigate the similarity of species in male and female diet and if this changed with scarcity. I also compared overlap within the sexes between seasons and years to test is *C. nictitans* reliably dispersed a subset of seeds regardless of food availability. I chose Schoener's index as it provides the most

accurate estimates over the greatest range of real overlaps when compared with other indices (Linton et al. 1981, Peres 1996).

Niche Width

I used the Shannon's diversity index to compare the dietary niche of *C. nictitans* for years, seasons and sex (Shannon and Weaver 1949, Kaplin et al. 1998b, Agostini et al. 2010). As above plant parts were put into three categories and scaled to 100%. In this index, higher values of *H* indicate higher niche width. It is calculated as:

$$H = -\sum_{i=1}^{R} p_i \, ln \, p_i$$

Where

$H =$ Index of species diversity

$s =$ Species richness

p_i = Proportion of individuals in sample belonging to the ith species

As Shannon's *H* is an index and not a true diversity I converted values using the exponential function to determine the 'effective number of species' (Magurran 2013). This value represents the diversity of the diet if all species were equally common, allowing for more intuitive understanding of values and for comparisons between studies using different diversity indices.

Pairwise comparisons were made using paired t-tests with an FDR correction to determine whether the niche width of different years, seasons or sexes were statistically significant from each other (Hutcheson 1970, Wahungu 1998). Differences in niche width would indicate that different sex or different food availability may alter the effectiveness of *C. nictitans* as a seed disperser from the perspective of the forest.

Time of Day

I used a Linear Mixed Model (LMM) to test the effect of time of day, food type, sex and interactions thereof on proportional consumption with date as a random effect. I performed an arcsine transformation on the response variable (consumption) to account for the use of proportional data (Zar 1999). Observations were categorised into eight one hour periods throughout the day, from 0600 to 1200 and from 1600 to 1800. As very few feeding observations were made between 1200 and 1600, this period was excluded to avoid the introduction of zero values (Zar 1999). Using a LMM allowed me to include date as a random factor to control for the lack of independence between observations taken on the same day. Not doing so would have resulted in pseudoreplication (Verbeke and Molenberghs 2009).

Significance was determined by conducting log-likelihood ratio tests using the ANOVA function in R, comparing the same model with the factor of interest included and excluded (Bolker, Brooks et al. 2009). This allowed me to investigate the interaction between time of day and proportional consumption of each food type, testing if observations matched the prediction of higher fruit consumption in the morning and leaf consumption in the evening.

Chi-square tests were used to compare observed consumption in each time period with the expected level of consumption. The expected value was calculated as proportional to the percentage of time foraging in that time period (Robinson 1984).

C. nictitans as a large seed disperser

Ranks

To investigate is *C. nictitans* consumed large fruited species in appreciable quantities, species of interest were identified from previous work conducted as NMFP. These were augmented by results from seed characteristic investigations, which were used to identify species with medium and large seeds. Consumption as determined as the proportion of independent feeding observations on fruit of that species was then ranked by sex between seasons and years. Due to difficulties identifying individual species *Ficus spp.* were grouped together and consider as a 'species' in analysis despite being a genus.

Preference

To investigate if *C. nictitans* demonstrated positive or negative preference for any species or part of a species I used Chesson's index (Chesson 1983). I choose Chesson's index over other electivity indices as it is unaffected to variation in the relative abundance of other items in the sample, allowing meaningful between sample comparisons (Lechowicz 1982). The index ranges from -1 (avoidance) to 1 (strong preference), with 0 indicating neutral selection. It is calculated by:

1.

$$\alpha_i = \frac{r_i \,/\, n_i}{\sum_{j=1}^{m} r_j / n_j}$$

Where

$\alpha_i =$ Manly's α (relative proportion of food species in diet)

$r_i =$ proportion of food species *i* in diet

$n_i =$ proportion of food species *i* in focal plots

$r_j =$ proportion of food species *j* in diet

$n_j =$ proportion of food species *j* in focal plots

2.

$$\varepsilon_i = \frac{m\alpha_i - 1}{(m-2)\alpha_i + 1}$$

Where

$\varepsilon_i =$ Electivity index

$\alpha_i =$ Manly's α

$m =$ total number of species

Indices were created using all known species that were present in both the phenological surveys (i.e. trees and shrubs) and in the *C. nictitans* diet. Three areas were examined:

1) Male and female preference for species in each year
2) Male, female and all observed *C. nictitans* preference in each season
3) All observed *C. nictitans* preference for food types (fruit, leaves, flowers) in each year

This allowed me to identify which species *C. nictitans* demonstrated a preference for and determine if it varied with availability of food or sex.

Selection for seed characterisation

To test if *C. nictitans* preferred specific seed characteristics I calculated selection ratios for characters of the 24 species measured during fruit collection. Following McConkey et al. (2002) I calculated selectivity as:

$$S_i = f_i / a_i$$

Where

$$Si = \text{Selection ratio of a given seed character trait}$$

$$f_i = \text{proportion of feeding observations on fruit with character trait of interest}$$

$$a_i = \text{relative proportion of availability of mature fruit with character trair of interest}$$

Availability (a_i) was measured using the same procedure as fruit availability above; as the product of phenology score and basal area (see chapter 2). I calculated selection ratios for each year as well as for the combined data of all years. This allowed me to investigate if selection was consistent for characters under differing levels of food availability. Selection ratios were calculated for four seed characteristics these were:

1. Seed number (1, 2-5, 6-20, ≥20)
2. Seed shape (0-0.2, 0.21-0.4, 0.41-0.6, 0.61-0.8, 0.8-1.0) (Figure 1)
3. Individual seed weight (<0.01 g, 0.011-0.5 g, 0.51-1 g, >1 g)
4. Seed to fruit volume ratio (0-0.02, 0.03-0.2, 0.21-0.4, 0.41-1.0) (Figure 2)

Each of the 24 species was placed in one category (shown in brackets) for each characteristic based off the average value of the 20 collected fruit (Table 1).

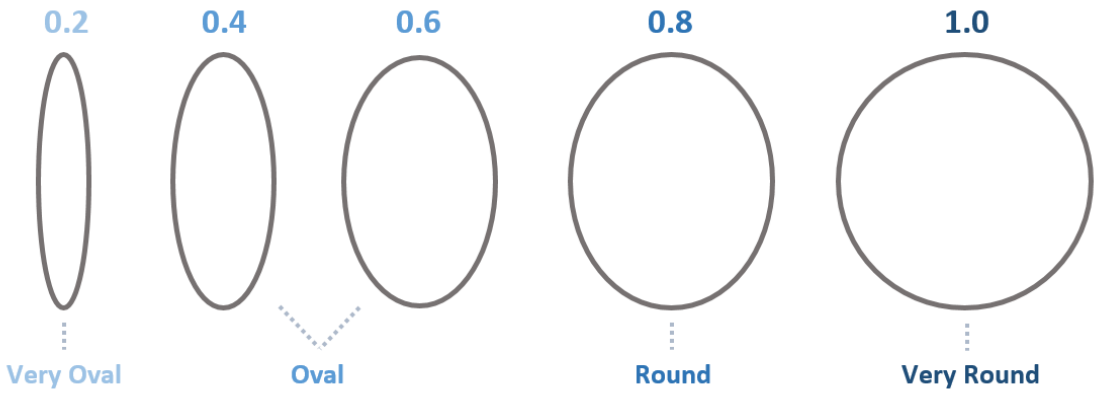


Fig 1. Diagram depicting seed shape classifications used in seed character selection analysis of 24 fruit species at NMFP. Species with a width to length ratio of 0-0.3 were classified as very oval, 0.3-0.7 oval, 0.7-0.9 as round and those with a ratio greater than 0.9 as very round.

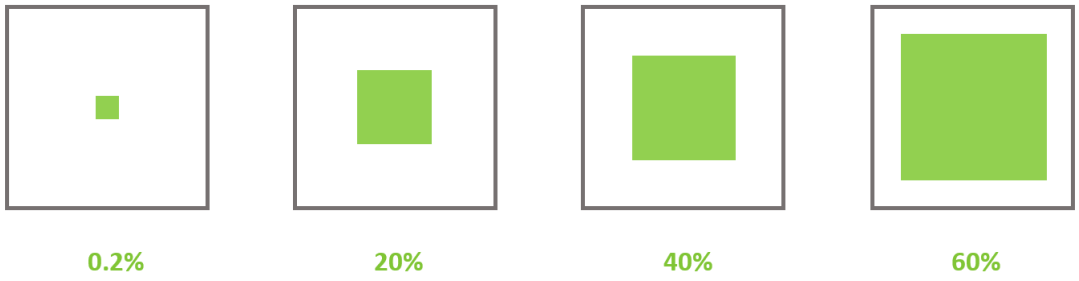


Fig 2. Diagram depicting examples of fruit to seed ratios used in seed character selection analysis of 24 fruit species at NMFP. Images shown are when seeds constitute 0.2%, 20%, 40% and 60% of total seed volume, covering a range from the data.

		All Years	2005	2006	2013-2014	Species
Seed Number	1	1.04	0.68	1.02	1.36	BEIL, POU, SANT, TRI, RAUV, MAC, EUG
	2-5	0.45	0.39	0.44	0.41	CHIO, GAR, POLY, SYMPH, SYZY, ANTH, CHRYS, H
	6-20	1.68	0.58	0.17	0.48	ALB, PARK, LAND
	≥20	1.25	1.83	1.02	1.61	ISO, FS, FL, ROTH, TAB, VOA
Seed Ratio	0-0.2	0.33	0.38	0.37	0.22	ALB, PARK, ROTH, ISO
	0.21-0.4	0.87	0.63	0.65	1.09	TAB, SANT, BEIL, POLY, POU, H, VOA, LAND, RAUV
	0.41-0.6	1.70	1.91	1.77	1.92	FL, SYMPH, GAR, ANTH, CHRYS, FS, TRI, SYZY
	0.6-0.8	0.02	0.01	0.00	0.00	CHIO, EUG
	0.8-1.0	0.00	0.00	0.00	0.00	MAC
Seed Weight	<0.01	1.84	2.48	1.55	2.47	FL, FS, POLY, MAC
	0.011-0.5	0.36	0.36	0.27	0.33	SYZY, ROTH, H, ANTH, CHRYS, TAB , CHIO, SYMPH, RAIV, VOA, EUG
	0.51-1	0.59	0.46	0.18	0.39	ALB, PARK, TRI, LAND
	≥1	1.06	0.80	1.26	1.15	BEIL, SANT, ISO, GAR, POU
Seed/Fruit	0-2	3.13	4.23	2.65	4.18	FS, FL, ALB
	3-20	1.50	1.16	0.89	1.93	SYMPH, TAB, POU, VOA, LAND
	20-40	0.03	0.03	0.02	0.03	ROTH, GAR, CHIO, TRI, H, SYZY, BEIL, RAUV, MAC
	>40	0.75	0.68	0.94	0.56	SANT, ANTH, CHRYS, ISO, POLY, PARK, EUG

Table 1. Seed characteristics for 24 species measures at NMFP, with selection ratio for each year and species with in each characteristic category. Species are **ALB** (*Albizia gummifera*), **ANTH** (*Anthonotha noldeae*), **BEIL** (*Beilschmiedia mannii*), **CHIO** (*Chionanthus africanus*), **CHRYS** (*Chrysophyllum albidum*), **EUG** (*Eugenia gilgii*), **FL** (*Ficus lutea)*, **FS** (*Ficus sur*), **GAR** (*Garcinia smeathmanii*), **H** (*Hannoa klaineana*), **ISO** (*Isolona* cf *deightonii*), **LAND** (*Landolphia buchananii*), **MAC** (*Macaranga occidentalis*), **PARK** (*Parkia filicoidea*), **POLY** (*Polyscias fulva*), **POU** (*Pouteria altissima*), **RAUV** (*Rauvolfia vomitoria*), **ROTH** (*Rothmannia urcelliformis*), **SANT** (*Santiria trimera*), **SYMPH** (*Symphonia globulifera*), **SYZY** (*Syzygium guineense*), **TAB** (*Tabernaemontana contorta*), **TRI** (*Trilepisium madagascariense*) and **VOA** (*Voacanga africana*). Characteristics investigate are average seed number per fruit (1, 2-5, 6-20, ≥20), seed shape calculated as a ratio of width to length (0-0.2, 0.21-0.4, 0.41-0.6, 0.61-0.8, 0.8-1.0), individual seed weight in grams (<0.01 g, 0.011-0.5 g, 0.51-1 g, >1 g), seed to fruit volume ratio expressed as a percentage (0-0.02, 0.03-0.2, 0.21-0.4, 0.41-1.0).

McConkey et al. (2002) noted that the traditional method of classifying all ratios >1 as overselection and those <1 underselection does not accurately assess boundaries. This because values close to one may not indicate significant feeding relative to abundance and thus be under neutral selection. To account for this they used assessed the boundaries more accurately by comparing proportional feeding to proportional availability using difference in binomial proportions. This method is however unsuited to my data, as instead of calculating relative availability as a presence/absence variable I used an analogue of relative crown area. Therefore, as graphing methods indicated data was best described by a Poisson distribution, I instead calculated 95% confidence Poisson intervals to assess boundaries. Values inside the interval were considered to be under neutral selections, those above overselection, and those below underselection. From this analysis I can infer which characteristics *C. nictitans* prefer under the assumption all other traits are not important.

Results

C. nictitans as a seed disperser

Overlap

Based on distribution of results, values an overlap greater than 80% was classified as high, values under 30% low, and in between moderate.

The amount of overlap between male and female diets varied between years. The highest overlap was seen in 2006, and the lowest in 2005 (Table 3). Overlap was high in 2006, moderate in 2013-2014 and low in 2005.

Overlap in diet between seasons varied between years for both females and males (Table 4). Males had high overlap between the wet and dry season in 2006, and moderate in both 2005 and 2013-2014. Females had moderate overlap between seasons in 2013-2014, and high overlap in 2005 and 2006. The amount of overlap between male and female diet during the wet season also varied

between years (Table 4). During the 2005 wet season there was only moderate overlap between male and female diet, where as in both 2006 and 2013-2014 the overlap between sexes was high. In all years male and female *C. nictitans* had moderate overlap in their diets during the dry season.

Males had lower overlap in their diet between years than females (Table 2). Males in 2005 had low overlap with males from both 2006 and 2013-2014. Dietary overlap for males in 2006 2with those from 2013-2014 was moderate. Female *C. nictitans* had moderate overlap in all comparisons. Between 2006 and 2013-2014 there was less overlap in female diets than males, however both sexes showed moderate overlap (Table 2).

When overlap was compared between sexes, within seasons, between years there was greater overlap than whole year comparisons. In all inter-year comparisons of diet during the wet season males showed moderate overlap between years, and females high. During the dry season all comparisons showed moderate overlap, except the comparison of female diet between 2006 and 2005 which demonstrated a high degree of overlap (Table 2).

		Sum		Wet		Dry	
		Male	Female	Male	Female	Male	Female
Years	2006-2005	0.0914	0.6594	0.7688	0.8125	0.7742	0.8378
	2006-2013	0.5570	0.4775	0.3032	0.8512	0.3032	0.3301
	2005-2013	0.0813	0.5546	0.3672	0.8247	0.3404	0.3426

Table 2. Overlap in diet between 2005, 2006 and November 2013 to October 2014 (2013) for male and female *C. nictitans* at NMFP. Overlap values are given for diet over the whole year (sum) and for during the wet and dry seasons. Values are calculated using Schoener's index of niche overlap (R_o) and using all known plant food items in *C. nictitans* diet. Highest value of overlap between years for each sex is shaded dark grey and lowest light grey.

	2005 Female	2006 Female	2013 Female
2005 Male	0.1461	0.0680	0.0796
2006 Male	0.6545	0.8828	0.4633
2013 Male	0.6017	0.5392	0.7051

Table 3. Overlap in female and male *C. nictitans* diet between 2005, 2006 and November 2013 to October 2014 (2013) at NMFP. Values are calculated using Schoener's index of niche overlap (R_o) and using all known plant food items in *C. nictitans* diet. Highest value of overlap for each sex is shaded grey.

		Male Wet vs Dry	Female Wet vs Dry	Wet Male vs Female	Dry Male vs Female
Year	2005	0.7442	0.8008	0.7960	0.5967
	2006	0.8490	0.8445	0.9087	0.7311
	2013	0.6078	0.5655	0.9485	0.6844

Table 4. Overlap in diet within years and the wet and dry season for Male and Female *C. nictitans*. Values are calculated using Schoener's index of niche overlap (R_o). Male and Female are the overlap of that gender between the wet and dry season. Wet and Dry are the overlap of the two genders in that season. Highest value of overlap between years for each sex is shaded dark grey and lowest light grey.

Dietary niche

The dietary niche of *C. nictitans* was significantly smaller in 2013-14 than in both 2005 ($t(4) = 9.9194$, $p < 0.001$) and 2006 ($t(4) = 5.509$, $p = 0.005$). 2005 and 2006 were not however significantly different from each other ($t(4) = 1.6145$, $p = 0.182$) (Table 5). This is evident in the effective number of food items consumed. In 2005 *C. nictitans* ate the equivalent of 18 species, in 2006 18.9 species, and in 2013-14 7.1 species (Table 6). Both male and females ate less than half the effective number of food items in 2013-2014, than in either other year.

There was no significant difference in the niche width of female and male *C. nictitans* ($t(2) = 1.3884$, $p = 0.229$). This was true of all inter- and intra- seasonal comparisons (Table 7). Though there was not a significant effect of season on dietary niche overall, females in both seasons of 2013-2014 demonstrated a notable

increase in width. During the wet season they ate over four times more effective food items than either other sex in an observed wet season. During the dry season they ate over three times more.

p = X *t* = *x*	2005	2006	2013
2005			
2006	0.182 *1.6145*		
2013	<0.001 * *9.194*	0.005 * *5.509*	

Table 5. Pairwise t-tests of Shannon's *H* for dietary niche of *C. nictitans* between years. Top value is *p* and the italicised value is *t*. For all comparisons df = 4.. An asterisks (*) is used to indicate significance. *p* values have been corrected for multiple comparisons using and FDR correction.

		Wet			Dry		
Year	Sex	# of food items	Effective # food items	Shannon's *H*	Number of food items	Effective # food items	Shannon's *H*
2005	Male	36	4.3	1.4485	44	6.0	1.7889
	Female	46	4.6	1.5169	56	7.1	1.9655
2006	Male	31	5.5	1.6967	29	4.4	1.4763
	Female	36	6.0	1.7864	33	4.2	1.4369
2013	Male	12	12.9	2.5573	5	2.5	0.9264
	Female	30	99.2	2.2178	17	22.8	3.126

Table 6. Comparison of Male and Female *C. nictitans* diet diversity in 2005, 2006 and the 2013 season at NMFP. Measures used are number of food items observed being consumed (leaves, flowers or fruit of all species), effective number of species and Shannon-Weaver diversity index (Shannon's *H*). Effective number of food items is rounded to one dp.

p = X		2005		2006		2013	
t = *x*		Wet	Dry	Wet	Dry	Wet	Dry
2005	Wet						
	Dry	0.087 *7.2921*					
2006	Wet	0.0262 * *24.3052*	0.197 *3.122*				
	Dry	0.713 *0.4842*	0.160 *3.8944*	0.142 *4.4144*			
2013	Wet	0.141 *4.4366*	0.298 *1.9777*	0.204 *3.0103*	0.102 *6.2043*		
	Dry	0.670 *0.51*	0.9069 *0.1473*	0.8322 *0.2698*	0.700 *0.5088*	0.824 *0.2846*	

Table 7. Pairwise t-tests of Shannon's *H* for dietary niche of all observed *C. nictitans* at NMFP at 2005, 2006 and between November 2013 and October 2014 (2013). Top value is *p* and the bottom value is *t.* For all comparisons df = 1. An asterisks (*) is used to indicate significance.

Variation with time of day

Results of the LMM indicated that *C. nictitans* consumed different foods types at different times of day ($\chi 2$ = 1948.457, *df* = 28, $p < 0.001$) (Fig 3). There was also a significant effect of the three way interaction of sex, time of day and food type, indicating that food type consumption varied differently for male and female *C. nictitans* ($\chi 2$ = 71.024, *df* = 35, $p < 0.001$) (Table 8).

Final Model: consumption ~ Sex + Time of day + Food type + Sex:Food type + Sex:Time of day:Food type + (1|date)	
Factor	**Significance**
Sex	$\chi2 = 48.323$, $df = 1$, $p < 0.001$
Time of day	$\chi2 = 1384.040$, $df = 7$, $p < 0.001$
Food type	$\chi2 = 4167.024$, $df = 4$, $p < 0.001$
Sex:Food type	$\chi2 = 48.323$, $df = 4$, $p < 0.001$
Sex:Time of day:Food type	$\chi2 = 71.024$, $df = 35$, $p < 0.001$

Table 8. Linear mixed effect model describing variation in *C. nictitans* diet at NMFP with time of day and level of significance for each factor or interaction. Levels of factors were sex (male, female), time of day (0600-0700, 0701-0800, 0801-0900, 0901-1000, 1001-1100, 1101-1200, 1600-1700, 1701-1800) and food type (fruit, leaves, flowers, arthropod, insect).

Chi-square tests indicated that, except for early morning (0600-07000, the composition of *C. nictitans* diet at all times of day was significantly different from what was expected based on food availability (Table 9). This was true of the combined data of all age and sex classes ($\chi2 = 5.458$, $df = 4$, $p = 0.2435$), as well as for the male ($\chi2 = 5.465$, $df = 4$, $p = 0.2429$) and female subsets ($\chi2 = 9.265$, $df = 4$, $p = 0.0548$) (Table 10).

	Combined		Female		Male	
Time	$\chi2$	p	$\chi2$	p	$\chi2$	p
0600-0700	5.458	0.2435	5.465	0.2429	9.265	0.0548
0701-0800	16.326	0.0026*	19.171	<0.001*	41.465	<0.001*
0801-0900	37.895	<0.001*	46.455	<0.001*	30.447	<0.001*
0901-1000	527.502	<0.001*	18.284	<0.001*	24.024	<0.001*
1001-1100	299.972	<0.001*	228.483	<0.001*	22.144	<0.001*
1101-1200	21.177	<0.001*	267.324	<0.001*	50.366	<0.001*
1600-1700	17.282	0.0017*	274.084	<0.001*	27.487	<0.001*
1701-1800	141.971	<0.001*	126.218	<0.001*	244.616	<0.001*

Table 9. Chi-square test result for proportional consumption on five food types (fruit, leaves, flowers, arthropods other) compared to expected frequencies for female, male and all observed (combined) in a troop of *C. nictitans* NMFP fom independent feeding observations in 2005 and 2006 at eight one hour time blocks throughout the day. An asterisks (*) is used to indicate significance at $\alpha = 0.05$.

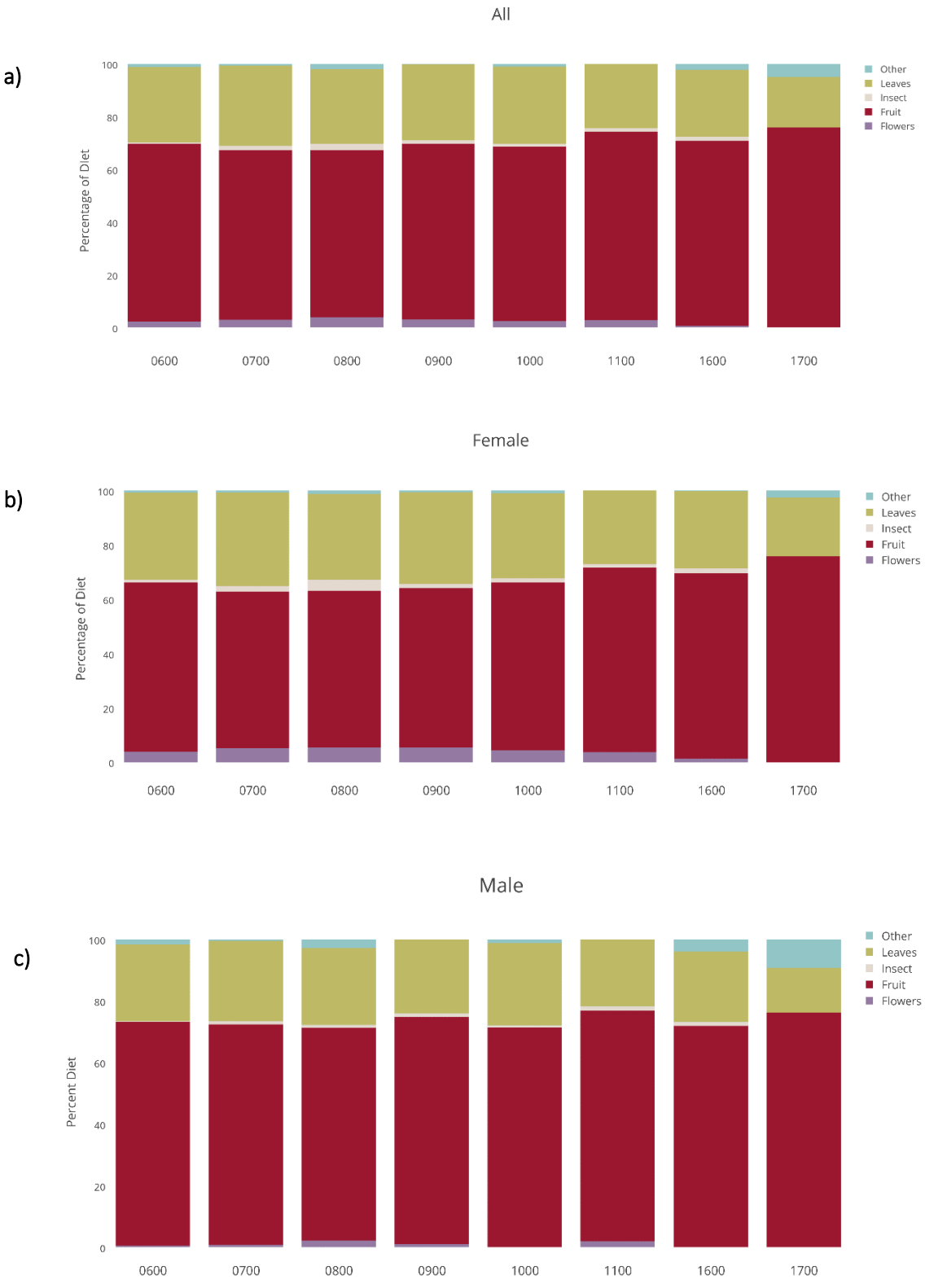


Fig 3. Average relative proportion of diet of five food types for **a)** all observed **b)** male **c)** female for a troop of *C. nictitans* in NMFP from independent feeding observations in 2005 and 2006 at eight one hour time blocks throughout the day. Insect refers to all arthropods. Time on x-axis indicates the start time of the one hour block of observation

C. nictitans as a large seed disperser

Species in diet

Large fruited species were identified from previous work undertaken at NMFP. Ihuma (2007) defined 'large' as species with a diameter greater than or equal to 15 mm, identifying 17 fruit species meeting this criteria. Of these *C. nictitans* was observed feeding on 15 during this study (Table 10). In 2013-2014 and 2006 *C. nictitans* consumed 11 of these, and in 2005 they consumed 12. Ten species were consumed in all years, two species were uniquely consumed in 2013-2014 (*Beilschiedia. mannii* and *Cordia millenii*) and one in 2005 (*Tabernaemontana contorta*). Two species were consumed in 2005 and 2006 but not in 2013-2014 (*Pterygot mildbraedii* and *Rothmannia urcelliformis).*

Average individual seed weights measured species ranged from <0.001g to 68.72g. Graphical means in conjunction with consideration of previous literature were used to group these into three categories 'small', 'medium' and 'large' (Howe and Smallwood 1982, Wunderle Jr 1997, Schupp et al. 2010). One large seeded species was identified that was not mentioned in Ihuma (2007). This was *Parkia filicoidea*, which was consumed by *C. nictitans* in 2005.

Species	Fruit type	Seed Size	2005	2006	2013-2014
Anthocleista vogelii	LF	M			
Anthonotha noldeae	LH	-	X	X	X
Beilschmiedia mannii	LF	-			X
Carapa oreophyla	LH	-			
Chrysophyllum albidum	LF	M	X	X	X
Cordia millenii	LH	-			X
Croton macrostachyus	LF	-	X		
Entenda abyssinia	LH	-			
Ficus Spp.	LF	S	X	X	X
Isolona cf *deightonii*	LH	L	X	X	X
Kigelia Africana	LH	-			
Parkia filicoidea	-	L	X	X	X
Pouteria altissima	LF	M	X	X	X
Pterygota mildbraedii	LF	-	X	X	
Rothmannia urcelliformis	LF	L	X	X	
Santiria trimera	LF	M	X	X	X
Strombosia scheffleri	LF	-	X	X	X
Symphonia globulifera	LF	-	X	X	X

Table 10. The presence of large fruit and large seeded fruit in *C. nictitans* diet at NMFP in 2005, 2006 and between November 2013 and October 2014. Grey crosses indicate that fruit from that species constituted <1% of proportional feeding observations that year, and black >1%. Fruit is categorised as either large hard (LH) or large fleshy (LF) based off Ihuma (2007). Seeds were classified as small (S) if they weighed less that 1g, medium (M) if they weighed between 1 and 5g and large (L) if they were over 5g.

	Small (<1g)	Medium (1-5g)	Large (>5g)
Species	*Macaranga occidentalis*	*Anthonotha noldeae* *	*Parkia filicoidea* *
	Polyscias fulva *	*Chrysophyllum albidum* *	*Rothmannia urcelliformis* *
	Rauvolfia vomitoria *	*Santiria trimera* *	*Tabernaemontana contorta* *
	Voacanga africana	*Pouteria altissima* *	*Isolona* cf *deightonii* *
	Eugenia gilgii *	*Garcinia smeathmanii*	
	Ficus Lutea *		
	Ficus Sur *		
	Albizia gumifera *		
	Syzygium guineense *		
	Chionanthus africanus		
	Landolphia buchananii *		
	Symphonia globulifera *		
	Hannoa klaineana		
	Trilepisium madagascariense *		

Table 11. Weight of individual seed of a subsample of fruit species available at NMFP. Weights are an average of 20 seeds for each species. Seeds were classified as small if they weighed less that 1g, medium if they weighed between 1 and 5g and large if they were over 5g. Species marked with an asterisk '*' were present in *C. nictitans* diet in 2005, 2006 or between November 2013 and October 2014. Species are ranked in increasing order of seed size within a column.

Ranks

In all years *Ficus* Spp. had highest consumption and *P. altissima* second highest (Table 12). This was true of combined diet for all observed *C. nictitans* as well as for the male and female subsets. Along with *P. altissima,* one other species with medium seeds was ranked in all years and for both sexes, this was *Anthonotha noldeae*. In 2006 a third medium seeded species was ranked, *Santiria trimera*. This was the fifth most consumed species for males and in combined data. One large seeded species, *Isolona deightonnii*, was ranked in 2005 and 2006. In 2006 it was the fifth most consumed species for females, and in 2005 it was fifth most consumed for both sexes and in combined data.

In 2005 and 2013-2014 though exact rank differed the same species were ranked for males and females within a year (Table 12). In 2006 there was one different species between the sexes. Four species were ranked

as a top five consumed species consistently in all years. 2005 and 2006 had one more species in common, meaning all species ranked in 2005 were also ranked in 2006. However as male and female ranks differed 2006 had one uniquely ranked species, *S. trimera* which was ranked fifth for males. In 2013-2014 one species, *Polyscias fulva*, was ranked that did not feature in either other year. It was ranked for both sexes and combined data.

	2005			2006			2013-2014		
	M	F	A	M	F	A	M	F	A
Anthonotha noldeae	4	3	3	4	4	4	4	3	3
Celtis gomphophylla	3	4	4	2	3	3	3	5	4
Ficus Spp	1	1	1	1	1	1	1	1	1
Isolona cf. deightonii	5	5	5		5				
Parkia filicoidea									
Polyscias fulva							5	4	5
Pouteria altissima	2	2	2	3	2	2	2	2	2
Santiria trimera				5		5			

Table 12. Top five consumed species for male (M), female (F) and all observed (A) *C. nictitans* for 2005, 2006 and 2013-2014. Rankings were determined by comparing relative proportion of species in independent feeding observations for that sex class.

In all years there was a larger number of ranked species in the dry season compared to the wet season. In 2005 there were six species ranked for at least one group during the wet season, and seven in the dry. For 2006 it was five species in the wet season and seven in the dry and in 2013-2014, five in the wet and nine in the dry. As a consequence of this, in all observed years male and female *C. nictitans* had more species in common in their top five rankings in the wet season compared to the dry. In all years males had an equivalent

amount of species in common between the wet and dry seasons, with the largest difference being only one species in 2005 (Table 13).

In all seasons *C. nictitans* had large fruit ranked in its top five most consumed foods, however how many and which species varied with year, season and sex. In 2005 wet season the same four species ranked for females, males and in the combined data. These were the small seeded *Ficus* spp., medium seeded *A. noldeae* and *P. altissima*, and large seeded *I. deightonnii*. During the dry season females had the same four species ranked as the wet, however for males and in the combined data *I. deightonnii* no longer featured. During the 2006 wet season, identical species were ranked as were in 2005 for both sexes and for the combined data. As with 2005, in 2006 species ranks were more variable during the dry season, though in 2006 all groups consumed four large fruited species. The combined data featured identical species as the wet season, for males *P. altissima* was no longer ranked and instead *Deinbollia* sp. featured, and for females medium seeded *S. trimera* was ranked instead of *I. deightonnii*. During the 2013-2014 wet season only two large fruited species were consumed, two less than previous years. For all groups these were *A. noledeae* and *P. altissima*. During the dry seasons males had identical species ranked, where as both females and the combined data a third featured. For females this was *Parkia filicoidea* and for the combined data *S. trimera*.

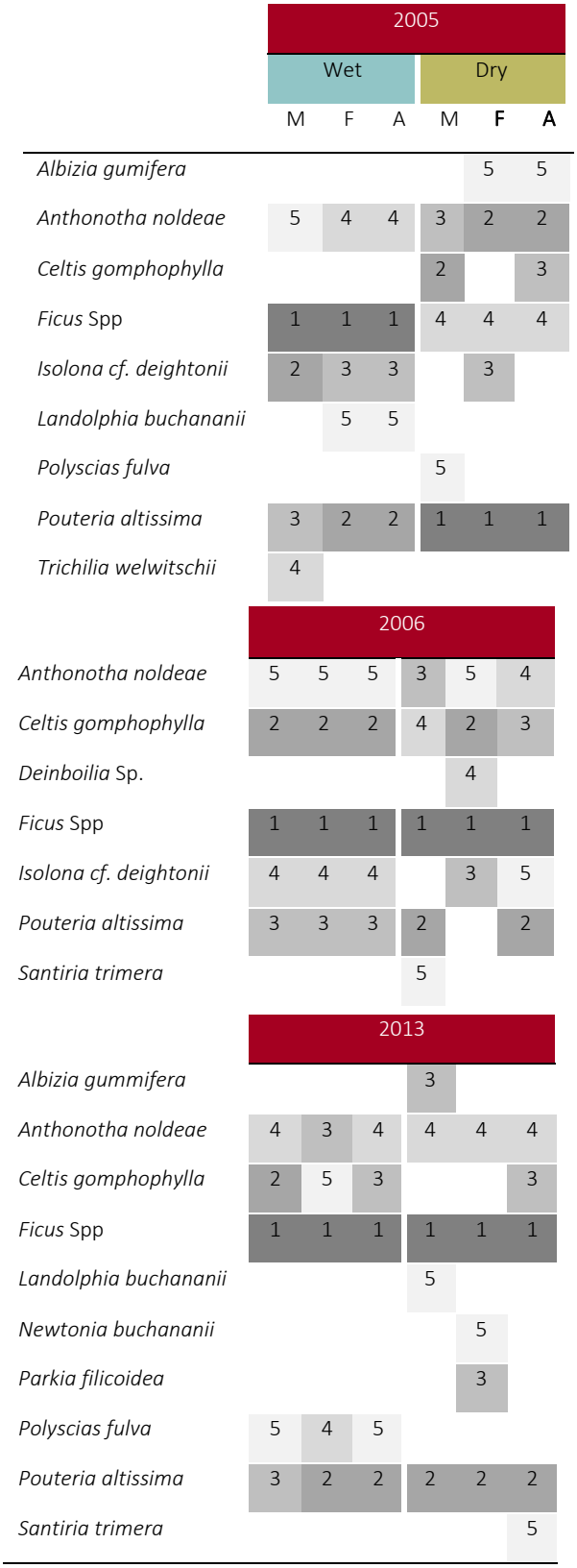


Table 13. Top five consumed species for male (M), female (F) and all observed (A) *C. nictitans* for 2005, 2006 and 2013-2014 by season. Rankings were determined by comparing relative proportion of species in independent feeding observations in a given season.

Preference

Based off the distribution of data preferences with an absolute value between 0 and 0.20 were categorised as neutral selection, 0.21 to 0.40 weak selection, 0.41 to 0.80 moderate, and 0.81 to 1 high.

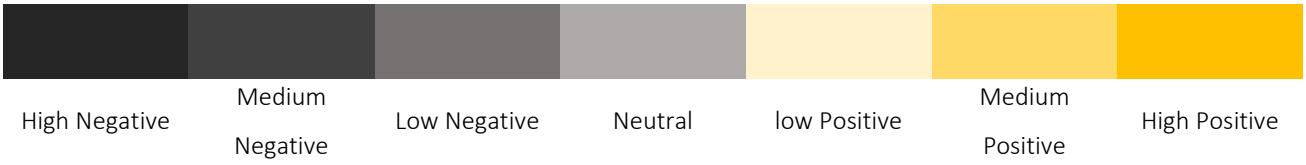


Fig 4. Key for colour codes on Chesson tables. Levels of selection are coded to a colour, with shades of grey used for negative values and yellow for positive. Based off the data, preferences with an absolute value between 0 and 0.20 were categorised as neutral selection, 0.21 to 0.40 weak selection, 0.41 to 0.80 moderate, and 0.81 to 1 high.

Both female and male *C. nictitans* showed preference for large fruited species in all years, however how many species and level at which they preferred these species with sex and year (Table 14). In 2005 females showed preference for three species, two of which were large fruited, *P. mildbraedii,* as well as small seeded *Symphonia. globulifera*. Males showed preference for an additional species, however it was not large fruited. Females in 2006 showed preference for one species only, *P. mildbraedii*. Males showed preference for two additional species, including *S. globulifera*. In 2013-2014 females showed preference for six species, the most of any year. Four of these were large fruited species, small seeded *Ficus* spp., medium seeded *A. nodae* and *P. altissima*, and large seeded *R. urcelliformis*. During the same year males showed preference for four species, only two of which were large, the least for males in any year. These two species were *Deinbollia* sp. and *Ficus* spp..

Preference also varied with season, with less preferred species in the dry season of 2005 and 2006, and more in 2013-2014 and in the combined data compared to the corresponding wet season (Table 15). In the 2005 wet season *C. nictitans* showed preference for four species and in 2006 two. In both periods they showed preference for the same two large fruited species *P. mildbraedii* and *S. globulifera*. In the 2013-2014 wet season all of the four species *C. nictitans* showed preference for were large; *A. noldae*, *Ficus spp.*, *P. filicoidea* and *P. altissima*. In the combined data *C. nictitans* showed preference for three species, two of which were

large. As with 2005 and 2006 these were *P. mildbraedii* and *S. globulifera*. Neither of the two species preferred in the dry season of 2005 were large. In 2006 *C. nictitans* showed preference exclusively for *P. mildbraedii*. Though there was an increase in the number of species preferred in 2013-2014 to five, the number of large species preferred dropped to two; *Ficus spp.* and *A. noldae*. The combined data also showed an increase to five species preferred, three of which were large. Unlike 2006 and 2013-2014, these were all species it had not shown preference for during the wet season; *Ficus spp., A. noldae* and *P. altissima.*

Both female and male *C. nictitans* preferences showed a similar trend as the combined data, with a decrease in the number of preferred species in the dry season of 2005 and 2006, and increase in 2013-2014 and in the combined data for all years. There were two discrepancies both males in 2005 and combined female data show equal preference between seasons. During the wet season of 2005 and 2006 both female and male *C. nictitans* showed preference for the same two large fruited species; *P. mildbraedii* and *S. globulifera*. Neither of these were preferred during the 2013-2014 wet season, nor in the combined data. Instead males and females showed preference for three large fruited species. For males these were *A. noldae*, *B. mannii* and *Deinbollia sp.* and females for *A. noldae,* along with *Ficus* spp. and *Parkia filicoidea.* During the dry season, males in 2005 maintained their preference for *P. mildbraedii* and *S. globulifera*. Females in 2005 and both sexes in 2006 however did not, instead showing preference for zero large fruited species. Males in 2013-2014 showed preference for five large fruited species, in addition to the three from the wet season these were *Ficus* spp. and *P. filicoidea*. Females in the 2013-2014 dry season showed preference for four large fruited species, two that were consistent with the wet season; *A. noldae* and *Ficus spp.*, and two that were not; medium seeded *C. albidium* and *P. altissima*. In the combined data during both seasons females show preference for the same two large fruited species, *Ficus* spp. and *S. globulifera.* Males showed preference for both of these in the dry season, along with two more large fruited species *A. noldae* and *B. mannii*. During the wet season the showed preference for only two of these *A. noldae* and *Ficus spp.*

Table 14. Chesson's index results for preference of the 32 known species in the *C. nictitans* diet as Ngel Nyaki for females and males in 2005, 2006 and November 2013 to October 2014. See figure 4 for key.

Table 14. Chesson's index results for preference of the 32 known species in the *C. nictitans* diet as Ngel Nyaki for females and males in 2005, 2006 and November 2013 to October 2014. See figure 4 for key.

a)


Male
Wet
Dry
Species
2005
2006
2013
All
2005
2006
2013
All
Albizia gumifera
Anthonotha noldae
Beilschmiedia mannii
Celtis gomphophylla
Chrysophyllum albidium
Cordia millenii
Croton macrostachyus
Deinbollia sp.
Entandrophragma angolense
Eugenia gilgii
Ficus sp.
Isolona cf deightonii
Lannea barteri
Memecylon afzelii
Newtonia buchananii
Parkia filicoidea
Polyscias fulva
Pouteria altissima
Pterygota mildbraedii
Rauvolfia vomitoria
Rothmannia urcelliformis
Santiria trimera
Schefflera abyssinica
Strombosia scheffleri
Symphonia globulifera
Syzygium guineense
Tabernaemontana contorta
Trichilia welwitschii
Trilepisium madagascariense
Uapaca sp.

b)


Female
Wet
Dry
Species
2005
2006
2013
All
2005
2006
2013
All
Albizia gumifera
Anthonotha noldae
Beilschmiedia mannii
Celtis gomphophylla
Chrysophyllum albidium
Cordia millenii
Croton macrostachyus
Deinbollia sp.
Entandrophragma angolense
Eugenia gilgii
Ficus sp.
Isolona cf deightonii
Lannea barteri
Memecylon afzelii
Newtonia buchananii
Parkia filicoidea
Polyscias fulva
Pouteria altissima
Pterygota mildbraedii
Rauvolfia vomitoria
Rothmannia urcelliformis
Santiria trimera
Schefflera abyssinica
Strombosia scheffleri
Symphonia globulifera
Syzygium guineense
Tabernaemontana contorta
Trichilia welwitschii
Trilepisium madagascariense
Uapaca sp.

C)

Table 15. Chesson's index results for preference of the 32 known species in the *C. nictitans* diet as Ngel Nyaki for males **(a)** and females **(b)** and all observed *C.nictitans* **(c)** in the wet and dry season of 2005, 2006 and November 2013 to October 2014. See figure 4 for key.

Table 16. Chesson's index results for preference of the 32 known species by part in the *C. nictitans* diet as Ngel Nyaki in the wet and dry seasons of 2005, 2006 and November 2013 to October 2014 (Referred to as 2013 in figure), as well as the average of three years. See figure 4 for key.

When species were consider as their different food parts, preference was shown for more large fruit in 2005 than 2006 or 2013-2014 (Table 16). In 2005 *C. nictitans* showed preference for the fruit of four species, three of which were large; *Ficus* spp., *I. deightonnii* and *S.scheffleri*. In 2006, *C. nictitans* exclusively showed preference for the large fruit of *C. albidium.* In 2013-2014 they showed preference for the fruit of two species, one of which was large; *B. mannii*. In the combined data of all years *C. nictitans* showed preference for the fruit of five species. This included three large fruited species *Ficus spp., I. deightonnii* and *P. altissima*. During all years, all large fruited species were observed with mature fruit during at least one season, therefore a lack of consumption does not solely reflect a lack of opportunity.

Selection for seed characteristics

Seed characteristics were not uniformly selected across years. During all years there was over selection for species with many small seeds, however in years with lower food availability there was an increase in selection on species with a single large seed. One characteristic, seed shape, did demonstrate uniform selection. Fruits with oval seeds, a ratio categorisation of either 0.21-0.4 or 0.41-0.6, were over selected in all years and in combined data. All other ratios were under selected.

In all years there was over selection for species with over 21 seeds, those with seeds that weighed less than 0.01g and where total seed volume was equal to or less than 2% of total fruit volume. Indicating that in all years *C. nictitans* sought out fruit which had many small seeds. However in 2006 and 2013-2014 there was also over selection for species with a single seed, and in 2006 for those with seeds weighing over 1g. In 2013-2014, species in this weight class were under neutral selection. Both weight classes were neutrally selected in the combined data and under selected in 2005. In 2013-2014 species with seed to fruit ratios between 3% and 20% and in 2006 those with seed to fruit ratios greater than 40% were neutrally selected. This indicates that in years with average and low availability there is greater selection for fruit with a single large seed than in years with high availability.

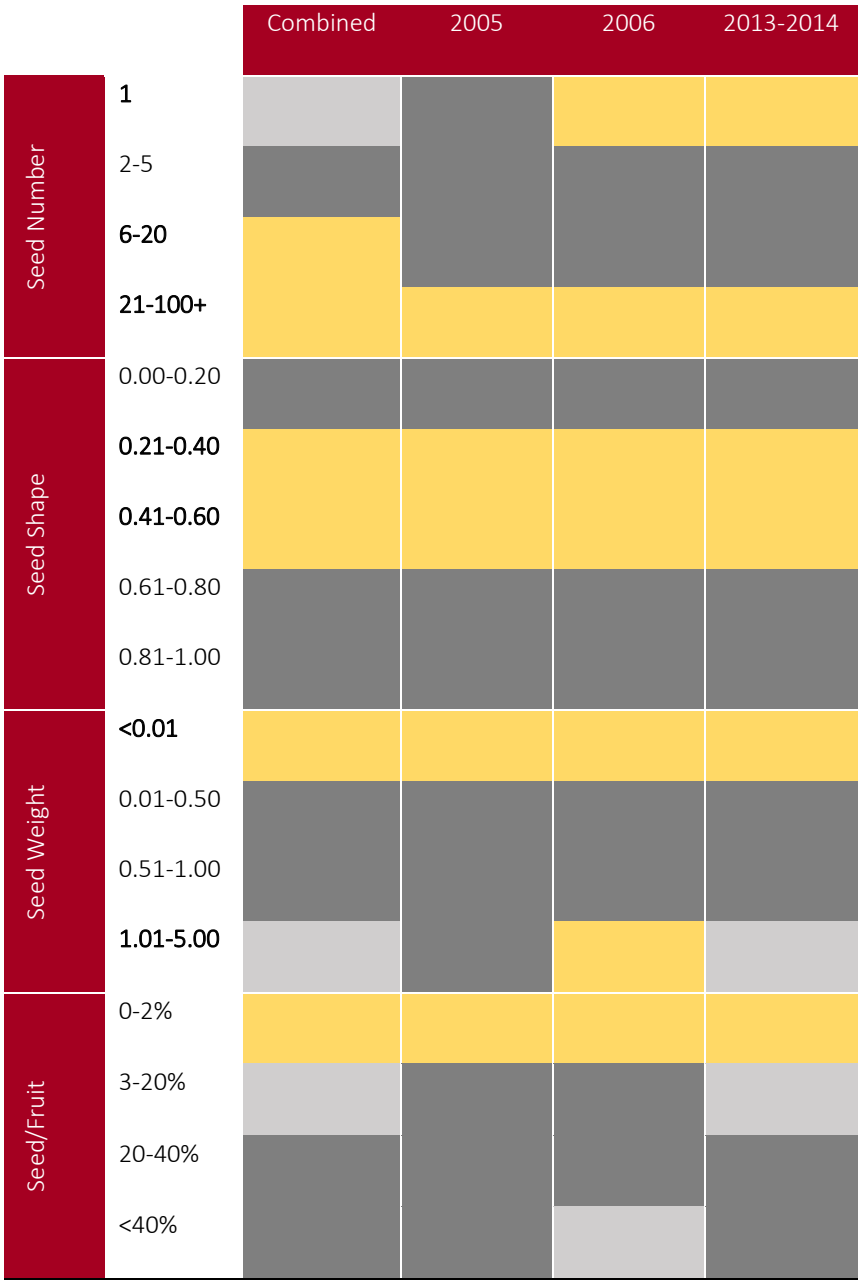


Table 17. Selection for different seed characteristics by *C. nictitans* at NMFP in 2005, 2006, between November 2013 and October 2014, and for combined data. Yellow indicates over selection, light grey neutral and dark grey under selection.

Discussion

Habitat disturbance is causing a global decline in the abundance of frugivores, with critical consequences for seed dispersal (Wilcox and Murphy 1985, Cardillo et al. 2005). Large seeded plants species are vulnerable as they depend on a restricted number of dispersers. Habitat regeneration is needed for both the conservation of biodiversity and the maintenance of the ecosystem processes (Parrotta et al. 1997, Sorensen and Fedigan 2000, Dirzo and Raven 2003, Moberg and Rönnbäck 2003). Animal mediated dispersal can help facilitate regeneration, therefore it is important to conserve large bodied dispersers in forest systems. However when this is not possible the use of surrogate dispersers may be able make up for loss (Albert et al. 2014). Cercopithicine monkeys have been proposed as a potential surrogate species, due to their ability to persist in degraded habitat and disperse large seeds via spitting. Specfically, Chapman et al. (2010) proposed that *C. nictitans* may serve as a surrogate disperser in degraded Afromontane forests which are threatened by the loss of their traditional large bodied dispersers; *P. t. elotti* and *Loxodonta Africana.*

I investigated the potential role of *C. nictitans* as a disperser of medium and large seeds: comparing overlap, niche width and preference between years; food consumption though out the day; relative consumption of large fruited species; and selection on different seed characteristics. I compared diet between seasons and over three years of varying availability. I also compared diets of female and male *C. nictitans*. This was to give an indication of the reliability and thus effectiveness of *C. nictitans* within NMFP, focusing on the most at risk medium and large fruited species to determine whether more focused study on their role as a surrogate disperser was needed.

Investigations indicated that *C. nictitans* demonstrate a degree of ecological flexibility that may impact on its effectiveness as a disperser of specific species. However it seems to show preference for and consume large amounts of particular species which included a number of medium and large seeded fruit in its diet. This means it may disperse certain species effectively, and may potentially also be an effective disperser from the

perspective of the forest. A concept further supported by evidence for selection of large seed traits in years of average and low availability.

C. nictitans as a seed disperser

Dietary overlap

The amount of overlap between years varied notably with sex. Female *C. nictitans* had higher overlap between 2005 (high availability) and 2006 (average), than either year had in comparison with 2013-2014 (lean). This fit predictions that overlap in diet of *C. nictitans* at NMFP would vary with inter-annual availability. Periods of low availability are associated with increased competition, which was expected to result in resource partitioning and broadening of dietary niche, possible due to the dietary flexibility observed in *C. nictitans'* diet (Chapter 2). Males did not follow this prediction however. They had lower overlap between 2005 and both 2006 and 2013-2014 than there was between 2006 and 2013-2014.

Though observed overlap was contrary to prediction, it followed the pattern seen in Lawes, Henzi et al. (1990). Studying the closely related *C. mitis*, they found greater similarity in diet during periods of low availability. That this pattern was found at NMFP and not in other studies, may be due to high level of disturbance including fragmentation and reduced forest area at NMFP causing particularly extreme periods of scarcity (Chapter 2). Previous work has shown during the dry season at NMFP female *C. nictitans* increase leaf consumption (Chapter 2). Leaves are more readily available than more costly fruit (Chapter 2), and therefore higher levels of leaf species preferred by *C. nictitans* are more likely to be available in all years and may be exploited as important secondary resources, potentially causing the observed similarity (Oates et al. 1980, Defler and Defler 1996, Conklin-Brittain et al. 1998). Being a submontane forest, NMFP may have had more nutritious leaves than other sites studied. As such a switch to folivory may not have been suitable in other field sites resulting in the employment of more varied strategies and less overlap (Schoener 1970, Gautier-Hion 1980, Waterman et al. 1983, Vitousek and Sanford 1986). To better understand resource use requires knowledge of nutritional values at NMFP and other sites, which was outside the scope of this study.

Comparisons of diet within seasons between years also did not always support predictions. Contrary to predictions, females' overlap was lower between dry seasons, when availability was relatively high. In comparison, females had high overlap between all wet seasons. Furthermore, males showed almost identical levels of overlap in the dry season as in the wet, rather than the predicted change. Unlike calculation of overlap between years, males showed higher overlap between 2005 and 2006 than either year showed with 2013-2014. This was in line with predictions that overlap would be higher between the years with average or higher availability, due to greater choice and less competition for resources. As before, this unexpected similarity may be due to a lack of choice in periods of scarcity. Females may be utilising as particular set of 'fallback' species in all wet season, resulting in high. More choice in the dry season, due to more species available in higher quantities could account for the differences in the dry season. That males diet was more even between seasons may be due to the competitive advantage over females, afforded to them by their size (Jones and Barmuta 1998, Butynski 2002, Albert et al. 2014). If any choice, such as for a preferred fruit species, was available males may be able to monopolise it throughout the year creating a more similar diet. (Chapter 2). Lower overlap in 2013-2014 may be caused by the extreme scarcity making these species unavailable.

Alternately, the difference could be due to males highly utilising a food in 2013-2014 that they did not in 2005 and 2006. This food may also be utilised by females in all wet seasons, explaining the similarity between years. During times of scarcity primates often utilise 'fallback foods'; foods with relative low nutrient value and high availability (Marshall and Wrangham 2007). Males' competitive advantage may give them better access to these foods during 2005 and 2006 wet season, resulting in the lack of overlap of these seasons with 2013-2014. Identifying potential fallback foods is important if *C. nictitans* is determined to be a surrogate disperser. Primate biomass is thought to be determined by food availability during times of scarcity (Gautier-Hion 1988, Hanya et al. 2006). Conservation planting efforts should therefore include these to help increase population numbers and encourage use of different forest areas (Meijaard et al. 2005, Marshall et al. 2009). Furthermore, it may be that despite only dispersing fallback species during lean years that *C. nictitans* may be having a large impact on seed dispersal. This could occur if fruit no longer has any other extant dispersers. In

such cases even a small amount of dispersal may have a large impact on species persistence, especially if dispersal is directed or long-distance (Nathan and Muller-Landau 2000, Wenny 2001). At NMFP fragmentation and regular lean periods may mean that fallback foods are regularly utilised, increasing the probability that dispersal is effective. Future studies should therefore identify potential fallback foods and their pattern of use.

Comparisons of female and male diet between years and seasons showed a similar pattern and were also contrary to predictions.

As intra-specific competition should increase during periods of scarcity, it was predicted that male and female overlap would be lowest during the lean year. Following prediction overlap was higher in 2006 than 2013-2014. However, with overlaps of 88% and 71% respectively both years were considerably higher than the 15% seen in 2005. Males in 2005 also showed much lower overlap with females in 2006 and 2013-2014, with less than 8% overlap, than males in 2005 and 2013-2014 showed with females in all years, which was always higher than 46%. The greater difference in male diet in 2005 from females in all other years may be due to greater food abundance allowing them to access and monopolise preferred foods only available in low quantities or absent in other years (Chapman 1987, Jones and Barmuta 1998, Butynski 2002, Albert et al. 2014). Further analysis of diet using the current data set into what species constituted the overlap would help determine why males in 2005 had such a different diet. This would be a valuable next step in identifying species that *C. nictitans* may disperse effectively.

Comparisons between sexes within a season of the same year also showed an opposite pattern to what was predicted. This is especially true of the 2013-2014 wet season which showed the highest level of overlap of any comparison, 95%. Males and females in 2005 showed the lowest. During the dry season overlap was again lowest in 2005, not highest as predicted. In all years there was a decrease in overlap in the dry season this was also not predicted, as food is more available in the dry than the wet season. This again fits with the findings of Lawes, Henzi et al. (1990) where low availability resulted in higher overlap due to less choice.

It is possible that results of overlap between male and female diet are influenced by the low sample size of males. In each year a maximum of two males were sampled, if even one of these males consumed a non-

typical it may result in inaccurate results (Zar 1999). However that male and females comparisons followed the general trend seen in combined, female dominated data; high overlap in low availability and low in high, suggests that the pattern seen is likely indicative of general trends across *C. nictitans* troops in the forest. The inclusion of only troop males may also have resulted in inaccuracies (Erhart and Overdorff 1999). The dietary needs of females means that troop movements and feeding patterns, including that of troop-males, are often different from solo-males whose foraging decisions only need account for themselves (Erhart and Overdorff 1999, Leca et al. 2003, Chapman and Russo 2007). Previous studies have found an annual female birth rate (number of female off- spring born per year) for *C. nictitans* of 0.33 (Fa et al. 1995). Troop size typically ranges from 12 to 30 individuals, with troops of up to 60 having been reported (Tutin 1999, Chapman et al. 2002, Eckardt and Zuberbühler 2004, Arnold and Zuberbühler 2008, Oates and Groves 2008). As there is typically only one male per troop this would mean there is a lot of solo-males in NMFP there is potentially a number of males eating a different diet than sampled (Gawaisa 2006). Different movement patterns, including higher use of fragments and longer day ranges may mean that this unsampled group of solo-males may be the most effective dispersers for forest regeneration (Erhart and Overdorff 1999, Leca et al. 2003, Chapman and Russo 2007). Solo-males were excluded from the current study due to a lack of resources. Low visibility at NMFP means locating and following solo-males is more difficult than for troops, meaning more time is required increasing costs (Altmann 1974, Setchell and Curtis 2011). Doing so however may provide invaluable information into *C. nictitans* role as a surrogate disperser.

Support for *C. nictitans* reliability as a seed disperser was therefore mixed. In six of the twelve comparisons between years they showed either close to or high overlap. However, in the remaining half overlap was moderate with around only 30% of food items shared. Current analysis included all food parts, a focus on fruit may give a better indication if *C. nictitans* are reliable dispersers. If all this 30% overlap was for fruit species it would paint a vastly more positive picture than if it was for leaves. To determine if it is a surrogate candidate would involve further analysis to see if there is overlap in the dispersal of medium and large seeded fruit species. Further investigation should determine if this is shared with *P. t. ellioitii¸* to see how well it may compensate if this species was lost from NMFP. Determining how much overlap there was between *P. t.*

ellioitii other primate dispersers could also help determine which species are at most risk. That there is a high level of overlap in half the comparisons, despite significant variation in availability, shows that this analysis and the extra work required is justified. Also the high overlap in times of scarcity suggests *C. nictitans* may reliably use certain fallback foods when food availability decrease, identifying these is important for helping conserve *C. nictitans* at NMFP. However, due to seasonal variation in availability and variation in yearly availability, it is plausible that *C. nictitans* utilises fallback foods frequently and thus may disperse them effectively (Marshall and Wrangham 2007, Schupp et al. 2010).

Niche Width

I predicted that there would be significant difference in niche width between years with less species consumed in the years of higher availability. This was because there was both a greater amount of food available and a larger range of species available (Chapter 2), thus *C. nictitans* could be more selective and focus on the species it preferred (Irwin, Raharison et al. 2015). As predicted there was a significant difference in niche width between 2013-2014 and other years, and no difference in niche width between 2005 and 2006. However contrary to predictions niche width was narrower in 2013-2014 than it was in either other year, with only the equivalent of 7.1 species consumed. Similar to overlap, this may be due to a decrease availability resulting in a lack of choice (Lawes et al. 1990). It is also potentially caused by diet analysis focusing on plant species. Previous work showed that during this period *C. nictitans* had a large increase in their proportional consumption of arthropods (Chapter 2). As these were not included in niche width analysis it is possible it did not capture the full diversification of diet in response to scarcity. However, as an increase in arthropod consumption does not directly increase *C. nictitans* effectiveness as a seed disperser, for the purposes of this study it is appropriate to view 2013-2014's niche as narrowed. A narrower niche means that it is likely a less effective disperser from the perspective of the forest as it is consuming and thus potentially dispersing less species (Shipley, Forbey et al. 2009).

Contrary to predictions there was no significant difference in male and female dietary niche width between years. However, though non-significant there was a clear increase in the effective number of species (the number of equally-abundant species needed to obtain the same mean proportional species abundance)

consumed in the wet season compared with the dry in 2013-2014. And an increase in 2013-2014 compared to other years. Though non-significant this fit with our prediction that niche width would increase in periods of scarcity. Furthermore, both increases were larger in female diet than male, which again fit with predictions.

Withing a season *C. nictitans* was observed consuming up to 56 plant based food items and u 99 effective species. This implies that it may disperse a wide range of species within the forest, and therefore may be, from the perspective of the forest, an effective disperser (Schupp et al. 2010). Dispersal effectiveness is not just quantative but also qualitiative. Future work must determine seed fates to truly determine if *C. nictitans* is an effective seed disperser at NMFP. Previous work has indicted that *C. nictitans* may have a positive effect on dispersal when defecating seeds, however more species need to be studied before this may be determined (Chapman et al. 2010). To determine how well *C. nictitans* may compensate for *P. t. ellioti* would also require knowledge of *P. t. ellioti's* niche width at NMFP, information which is not currently available.

Time of Day

Previous studies found that most primate species vary diet with time of day, to better meet changing energy requirements throughout the day. Typically fruit is consumed in the morning and/or late afternoon, and leaves in the afternoon (Gautier-Hion 1980, Robinson 1984, O'Brien and Kaiser 1985, Tweheyo et al. 2004). Similar to previous studies, the relative amount of each food type eaten at different days of day varied, with all periods except the early morning (0600 to 0700) different from the expected diet. This was true of females, males and for the combined data of all age and sex classes. However contrary to prediction fruit did not predominantly occur in the morning instead it increased over the day peaking in the evening (1700 to 1800). Leaf consumption by males was relatively evenly distributed throughout the day, however female and scombined data shows a trend toward predominantly morning consumption.

In a review of 15 primate species Chapman and Chapman (1991), identified five species with high afternoon consumption of fruit: *Callicenus toruatus* (collard titi), *Colobus guereza* (mantled guereza), *Hylobates syndactylus* (siamang), *H. lar* (lar gibbon) and *Pongo pygmaeus* (Bornean orangutan). Only one of these, *C. guereza* was observed to have a peak in the evening but not the morning, i.e. the same pattern as in my data.

This was attributed to it possessing a sacculated stomach allowing for fermentation of leaves and subsequent release of energy over periods of up to 10 hours (Chapman and Chapman 1991, Milton 1998). This explanation does not fit for *C. nictitans* due to their simple guts (Chivers and Hladik 1980). A recent study by Matsuda et al. (2014) used cluster analysis and found that most non-human primates fruit consumption peaked in the afternoon. Furthermore that the time of day fruit peaked and overall feeding rhythm was not reflective of overall diet strategy, suggesting other factors may be at play. As the study was limited in the number of studies on each species, it is possible ecological factors such as food availability played a role. Morning peaks in fruit consumption were often season or otherwise transient. It may therefore be that by averaging data over two years I lost this effect (Matsuda et al. 2014).

The lack of fruit consumption in the morning be *C. nictitans* at NMFP may be a reflection of lower fruit availability (Chapter 2) and the typically more nutritious leaves in montane forests (Gautier-Hion 1980, Harrison 1983). Lower encounter rates may decrease the relative value of a fruit, while simultaneously the increasing relative value of leaves due to their nutrient content, changing optimal foraging dynamics (Garber 1987). To understand this requires a better understanding of how *C. nictitans* utilise the forest and the spatial dynamics of availability of fruit in NMFP, as well as nutrient content of different food items and species.

Time of day comparisons were performed using one troop in two years of comparable availability, it may be that this result is merely a quirk, which could be determined by gathering data on diurnal diet variation for more troops across more variable years (Zar 1999, Matsuda et al. 2014). Futhermore, as this analysis focused on relative amount of time spent feeding on each food item, it may be that despite spending less time eating fruit in the morning compared to other food types, *C. nictitans* may be eating a greater mass of fruit compared to the rest of the day. This would be best calculated after the mean weights of each species is known (Rothman et al. 2012). They may also be eating higher quality food in the morning, resulting in a higher energy intake than in the afternoon (Carlson et al. 2013). This would best be investigated once nutrient values of species are known, but may be indicated by varying consumption of species throughout the day and consistent use of a subset of fruit species in the morning.

If *C. nictitans* however does predominantly consume fruit in the afternoon it may have negative consequences for its role as an effective seed disperser. In diurnal primates, afternoon fruit consumption is more likely to result in clumped seed distribution, as seeds are mostly defecated once primates are resting at night (Chapman and Russo 2007). Clumped distributions increase intra-specific competition between seeds and lower the probability that seeds are deposited in a suitable micro-habitat (Chapman and Russo 2007, Schupp et al. 2010). If some seeds are spat during transit in the afternoon it may alleviate this effect somewhat by creating a more varied seed shadow (Kaplin et al. 1998a). Though some studies have found beneficial effects of spitting (Lambert 2001, Balcomb and Chapman 2003, Gross-Camp and Kaplin 2011), it has also been found that most spat seeds are found within 10m of the parent tree, and are subsequently unlikely to escape its shadow (Lambert and Garber 1998, Albert et al. 2014). As such, a study into deposition of seeds by *C. nictitans* at NMFP is required before they can be considered a suitable surrogate disperser. This should consider solo-males who due to freedom from female dietary influence, may consume more fruit and consume it more consistently throughout the day. Females have previously identified as both eating more leaves than males and increasing proportional consumption in response to scarcity, indicating they may be an important food sought out in their diet (Chapter 2). Males did not increase leaf consumption in times of scarcity, instead eating a greater proportion of arthropods, it follows that if not associated with females, males may spend less time eating leaves and instead potentially demonstrate the expected pattern of morning fruit consumption. This would potentially increase the quality of seed dispersal by *C. nictitans* and thus effectiveness (Schupp et al. 2010).

C. nictitans as a large seed disperser

Consideration of both large fruit size in conjunction with seed size lead to the identification of 18 fruit species in NMFP which may be effected by the loss of wide gaped seed dispersers. Of these *C. nictitans* was observed feeding on 16 species during the study, as such large fruited species made up half of the 32 consumed species identified in their diet (Chapter 2). Not all species were consumed every year, however ten species were consumed to some degree in all three years. Of these at least seven had medium or large seeds, however as

of yet seed data for all species within *C. nictitans* diet is yet to be gathered. As such it is likely this number will increase.

C. nictitans have relatively high biomass at NMFP, as they appear to be consuming a notable amount of large fruited species, it is highly likely that they are impacting of dispersal of medium and large seeded species in either a positive or negative capacity. This supports their potential as a surrogate disperser, but equally due to our current lack of knowledge could also support a role as a significant seed predator (Chapman 1989, Lambert and Garber 1998, Schupp et al. 2010). A more in depth study of frequency of visitation and seed fate is needed to differentiate between the two. Currently only two of the identified species, *I. deightonnii* and *S. trimera*, have been investigated in relation to *C. nictitans* seed dispersal (Chapman et al. 2010). Chapman et al. (2010) found that gut passage through *C. nictitans* had a positive effect on germination rates of both seed species, spitting however had a neutral effect on *I. deightonnii* and a negative effect on *S. trimera.* This was determined via experiment and did not take into account the microsite the seed was deposited in (Chapman et al. 2010). Repeating this experiment on a larger scale including more species would be a potential start to understanding *C. nictitans* role on large fruited species recruitment.

Interestingly, in 2013-2014 *C. nictitans* was observed feeding on *Cordia milleni*. Previous studies and unpublished work at NMFP has indicated that *C. millenii* is only dispersed by *P. troglodytes* (Nishida 2002, Babweteera 2009, Thia 2014). As a result at NMFP it has been identified that *C. millenii* is experiencing arrested recruitment (Thia 2014). The possibility that *C. nictitans* may consume and disperse even a small amount of these seeds thus warrants further investigation, specifically if they move seeds in to suitable microhabitats with both sufficient light and moisture for seedling establishment (Chapman et al. 1999). It is possible that due to previous studies occurring in 'average' or 'high' years this potentially important interaction has been missed.

Ranks

For both sexes in all years the highest proportion of feeding observations occurred on *Ficus* spp.. Ficus, unlike other species, was included in the analysis as a genus. It is probable that by combining a number of species its

rank was artificially inflated. Though *Ficus* spp. were identified in analysis as having large fruit, both species (*Ficus lutea* and *Ficus* sur) which had their seed characteristics measured had very small seeds typical of the genus. Due to their fleshy nature and these small seeds it is likely a number of small gaped species at NMFP can also disperse *Ficus* spp.. Furthermore, previous studies have also observed dispersal of *Ficus* spp. by other primate at NMFP, and it is therefore unlikely the genus is experiencing dispersal crisis (Agmen et al. 2010, Dutton and Chapman 2015). As such the can be excluded in discussion of the amount of large fruited species dispersed by *C. nictitans,* thus avoiding the complication of comparing consumption of a genus with that of species. Interestingly, despite its advantage as a genus, *Ficus* spp. was ranked only 4th in the 2005 dry season for both sexes. Medium seeded *P. altissima* instead was the highest ranked species.

In all years, three large fruited species with either medium or large seed (i.e. that were not *Ficus* spp.) were ranked in the top five foods, based on proportion of independent feeding observations. This fit with my prediction that *C. nictitans* would be consuming and potentially dispersing a number of large fruited species. Contrary to my prediction, their ecological flexibility did not prevent a high proportion of these being shared between years. With two species, *Pouteria altissima* and *Anthonotha noldae,* ranked in all years This suggests that *C. nictitans* may reliably disperse these species, in relatively large quantities regardless off scarcity and thus may be an effective disperser (Schupp 1993).

When diet was considered in terms of proportional consumption by females and males in the different seasons of each year, large fruited species still featured prominently in rankings. There was however, less consistency in which species featured. Three species frequently feature in male and female rankings. *P. altissima*, *A. noldae* and *I. deightonnii.* Defecation by *C. nictitans* has previoulsy been shown to improve germination rates for *I. deightonnii* (Chapman et al. 2010). The remaining two species are strong candidates for targeted investigation as to if *C. nictitans* effective as a disperser.

In 2013-2014 rankings less large fruit species were consumed than in other years. Large fruit are costly and likely less available during periods of scarcity such as 2013-2014 (Chapter 2). Two large fruited species, *P. altissima* and *A. noldae* still ranked for both sexes in each season. Interestingly females also consumed a large

proportion of *Parkia filicoidea* during the dry season. This was not featured in any other ranking but is a species known to be found in *P. t. elloitii* faecal deposits. Its high consumption in 2013-2014 suggest it may be a fallback food for *C. nictitans*. Therefore it is also a species worthy of further study.

Ranks were based off independent feeding observations and not adjusted for fruit weight, this means that they may not correctly represent the proportion of each food in the diet due to differences in food handling times (Rothman et al. 2012). Future studies should correct for both fruit weight and handling time, once data is available for all species. However that was not possible for the current study. Furthermore, as male ranks have a maximum sample size of two for each year, rankings may reflect diet of an outlier. This seems unlikely though due to the similarity in species ranked in 2013-2014, where two different males were observed, to 2005 and 2006 (Zar 1999).

Preference

Understanding preference can help identify species *C. nictitans* may be effective dispersers for as they will seek out and preferentially consume these species, fulfilling the spatial requirement of reliable dispersal (Kaplin and Lambert 2002). Based off previous studies, it was predicted that *C. nictitans* would prefer a number of large fleshy fruits (Gautier-Hion 1980, Kaplin and Moermond 2000, Brugiere et al. 2002, Kaplin and Lambert 2002, Chapman and Russo 2007), however as scarcity increased so would competition, resulting in changes in *C. nictitans* diet including a decrease in the number of preferred large fruit species as availability and access to these species both decreased (Schoener 1970, Gautier-Hion 1980, Yeager 1989, Kaplin, Munyaligoga et al. 1998).

As per prediction *C. nictitans* showed preference for large fruited species in all years, and the amount varied with sex and year. Large fruited species preferred were more consistent between 2005 and 2006 than in 2013-2014, with *P. mildbraedii* and *S. globulifera* featuring in both years. Contrary to predictions, females in 2013-2014 showed the greatest amount of preference of any sex in any year. Despite 2013-2014 females having preference for six species, four of which were large fruited species, the only overlap in preference was with males in the same year for *Ficus* spp.. Males also demonstrated unique preference in 2013-2014, being

the only group to show preference for *Deinbollia* sp.. The increase in number of preferred species in 2013-2014 and the high number of unique preference may reflect a lack of availability of preferred food during this lean year, as Chesson's index is sensitive to rare species (Lechowicz 1982, Chesson 1983). Similarly, greater preference could also be caused by local abundance in a time of overall rarity. It may be that these species were abundant in *C. nictitans* home range and as a result highly consumed during 2013-2014, whilst being rare on phenology transect and in the forest overall. Future studies could avoid this by tracking local availability in *C. nictitans* diet (Lechowicz 1982). Alternatively it may reflect a change in dietary strategy to cope with scarcity (Agetsuma and Nakagawa 1998, Kaplin and Moermond 1998). They may be targeting different nutrients or switching to more predictable fruit species, as would be suggested by the observed switch in dietary strategies and lower overlap of 2013-2014 season with those in other years.

Seasonal preferences reflected yearly data, with preference for *P. mildbraedii* and *S. globulifera* in both 2005 and 2006, and for unique species in 2013-2014, including *A. noldae* and *P. altissima.* In 2005 and 2006 there was a decrease in number of preferences with total food availability, with less preferred species in the dry season. Notably, females in the dry season of both years showed preference for zero species. This may be as high availability meant in 2005 and 2006 there was an abundance of high quality foods (Marshall and Wrangham 2007). Therefore *C. nictitans* did not need to be selective, eating a range of larger fleshy fruit species, decreasing the likelihood any one would be classified as a in preference (Chesson 1983, Lawes et al. 1990). The opposite was seen in 2013-2014 with an increase in number of species preferred in the dry season. This may be due to the lower availability in the wet season limiting *C. nictitans* ability to exercise choice, as indicated by findings in overlap and niche width above (Lawes et al. 1990). As previously discussed the increase in the dry season may be due to utilisation of fallback foods (Marshall and Wrangham 2007).

Two species consumed in high quantities were only preferred in 2013-2014, *P. altissima* and *A. noldae*. For *A. noldae* this is potentially is due to a decrease in availability while a maintaining a similar level of consumption. Previous work showed that in all years in made up around 10% of *C. nictitans* diet and that relative consumption was higher in 2006 than 2013-2014 (Chapter 2). On first impression this may indicate that *C.*

nictitans is reliably dispersing this species, regardless of scarcity and therefore may play an important role in its recruitment (Schupp et al. 2010). This would however only be true is *C. nictitans* predominantly consumed the fruit of *A. noldeae.* Aas it is hard, and appears adapted to wind dispersal, this seems unlikely and instead consumption of fruit by *C. nictitans* was more likely seed predation (Wenny 2000). Further supporting this is the observation that consumption by *C. nictitans* of *A. noldae* in all years was predominantly on leaves (see Chapter 2). However, as small amounts were eaten the fate of these seeds should be determined (Schupp et al. 2010). This could be done by looking for intact seeds in *C. nictitans* faecal matter.

Overall these results suggest that in years with at least average availability, *C. nictitans* may consume large amounts of *P. mildbraedii* and *S. globulifera* relative to availability. Fulfilling the spatial requirement of effective dispersal and as such it may be a reliable dispersers of these large fruited species (Schupp et al. 2010). However their reliability is negatively impacted by the lack preference in lean years, which may potentially be due to a lack of availability or use instead of fallback foods (Marshall and Wrangham 2007). Determining this will give a better picture of *C. nictitans* effectiveness as a disperser and thus suitability as a surrogate disperser of medium and large seeds.

Selection

In all years *C. nictitans* showed selection for fruit species with small, numerous, oval seeds associated with relatively large proportion of fleshy reward. It therefore seems likely that these represent their preferred type of seed when available. These characteristics are similar to findings pf previous studies on primate fruit and seed characteristic preferences (Stevenson 2004). However, in both the average and lean year there was also selection for species with a single, large, oval seed. Undigested seeds bulk out the stomach without providing a source of energy (Corlett and Lucas 1990, McConkey and Brockelman 2011). During periods of low food ability food is often also of a lower quality therefore more food is often also needed, however due to lower availability it is also harder to find (Garber 1987, Overdorff 1996, Tutin et al. 1997). This means that during these periods primates though spend more time foraging and consume a greater mass of food they may still have lower energy and nutrient intake (Overdorff 1996). As such they may be under greater pressure to minimise eating seeds, as well as to lower food handling time. A single large seed may be easier to remove

and spit than many small seeds. To determine this would require timing individual fruit handling time of the different species and which was outside the scope of this study.

Having a single seed may also be associated with other plant characteristics, such as lipid content or presence of secondary metabolites, that may increase or decrease consumption (Stevenson 2004). A confounding variable could explain the observed pattern (Zar 1999). Characteristics associated with the flesh would be more visible and apparent, and therefore may be more likely to be selected for than seed. For some fruit characteristics, such as sugar content, thickness of outer protection and secondary metabolites, it would be difficult for the primate to not experience them prior to seed characteristics, unless fruit is being manually removed, and in such a case it is likely this is being done so they may predate on seed (Gautier-Hion et al. 1985). Future studies should be conducted analysing fruit characteristics along with seed characteristics. Investigating at selection not just on a single characteristic but on a number of different fruit and seed characteristics simultaneously. A species may have both over- and under- selected characteristics and understanding how these are weighted in selection will help determine how much the selection on large seeds actually translates into consumption of large seeded species (McConkey et al. 2002).

Throughout time there is more average and low availability years combined than there is high years. If during these periods *C. nictitans* does select for large seeds, and does not predate on them they may be a valuable surrogate disperser for *P. t ellioti* at NMFP. Future studies are needed to investigate a larger sample of fruit species to see if this trend is consistent. This should be done in conjunction with fruit characteristics to control for confounding variables. It may be that seed characteristics are selected on second to other more salient characteristics, investigating fruit characteristics along would seed would help determine this.

Conclusion

Evidence for *C. nictitans* as both an effective seed disperser in NMFP and surrogate for *P. t ellioti* were mixed. Contrary to all predictions, it appears *C. nictitans* is a more reliable disperser, who is more effective from the perspective of the forest in years of low availability than average of high. This may however be due to inclusion of all food types, and before any firm conclusion is made on *C. nictitans* status as a seed disperser anylises should be repeated focusing on fruit consumption only. Results from preference indicate that this increased reliability may be due to use of fallback foods. Understand *C. nictitans* diet involves identifying these food, and when they are used. Future studies should also look at the role of nutrients in food choice, diet of solo males and fruit handling time. These will give a clearer picture of *C. nictitans* as seed disperser at NMFP. As it was found that over half *C. nictitans* diet was large fruited species, that they consumed large quantities of these and appeared to seek out a subset for consumption further research into *C. nictations* is warrented. Including investigation of identified species directly measuring the number of new adults produced by the *C. nictitans* activities as a disperser.

References

Agetsuma, N., and N. Nakagawa. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. Primates **39**:275-289.

Agmen, F. L., H. M. Chapman, and M. Bawuro. 2010. Seed dispersal by tantalus monkeys (Chlorocebus tantalus tantalus) in a Nigerian montane forest. African Journal of Ecology **48**:1123-1128.

Agostini, I., I. Holzmann, and M. S. Di Bitetti. 2010. Are howler monkey species ecologically equivalent? Trophic niche overlap in syntopic Alouatta guariba clamitans and Alouatta caraya. American journal of primatology **72**:173-186.

Albert, A., K. McConkey, T. Savini, and M.-C. Huynen. 2014. The value of disturbance-tolerant cercopithecine monkeys as seed dispersers in degraded habitats. Biological Conservation **170**:300-310.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour **49**:227-266.

Arnold, K., and K. Zuberbühler. 2008. Meaningful call combinations in a non-human primate. Current Biology **18**:doi:10.1016/j.cub.2008.1001.1040.

Babweteera, F. 2009. *Cordia millenii*: on the risk of local extinction? African Journal of Ecology **47**:367-373.

Balcomb, S. R., and C. A. Chapman. 2003. Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecological Monographs **73**:625-642.

Borokini, T., F. Babalola, T. Amusa, S. Ivande, Z. Wala, O. Jegede, D. Tanko, and J. Ihuma. 2012. Community-based Forest Resources Management in Nigeria: Case study of Ngel Nyaki Forest Reserve, Mambilla Plateau, Taraba State, Nigeria. Journal of Tropical Forestry and Environment **2**:69-76.

Brugiere, D., J.-P. Gautier, A. Moungazi, and A. Gautier-Hion. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology **23**:999-1024.

Butynski, T. M. 2002. The guenons: Diversity and adaptation in African monkeys. Kluwer Academic, New York.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Carlson, B. A., J. M. Rothman, and J. C. Mitani. 2013. Diurnal variation in nutrients and chimpanzee foraging behavior. American journal of primatology **75**:342-349.

Chapman, C. 1987. Flexibility in diets of three species of Costa Rican primates. Folia Primatologica **49**:90-105.

Chapman, C. A. 1989. Primate seed dispersal: the fate of dispersed seeds. Biotropica **21**:148-154.

Chapman, C. A. 1995. Primate seed dispersal: coevolution and conservation implications. Evolutionary Anthropology: Issues, News, and Reviews **4**:74-82.

Chapman, C. A., and L. J. Chapman. 1991. The foraging itinerary of spider monkeys: when to eat leaves? Folia Primatologica **56**:162-166.

Chapman, C. A., L. J. Chapman, M. Cords, J. M. Gathua, A. Gautier-Hion, J. E. Lambert, K. Rode, C. E. Tutin, and L. J. White. 2002. Variation in the diets of Cercopithecus species: differences within forests, among forests, and across species. Pages 325-350 The guenons: Diversity and adaptation in African monkeys. Springer.

Chapman, C. A., L. J. Chapman, L. Kaufman, and A. E. Zanne. 1999. Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. African Journal of Ecology **37**:81-92.

Chapman, C. A., L. J. Chapman, R. Wangham, K. Hunt, D. Gebo, and L. Gardner. 1992. Estimators of fruit abundance of tropical trees. Biotropica **24**:527-531.

Chapman, C. A., and D. A. Onderdonk. 1998. Forests without primates: primate/plant codependency. American journal of primatology **45**:127-141.

Chapman, C. A., and S. E. Russo. 2007. Primate seed dispersal. Primates in perspective. New York: Oxford University Press:510-525.

Chapman, H. M., S. L. Goldson, and J. Beck. 2010. Postdispersal removal and germination of seed dispersed by Cercopithecus nictitans in a West African montane forest. Folia Primatologica **81**:41-50.

Chesson, J. 1983. The estimation and analysis of preference and its relatioship to foraging models. Ecology **64**:1297-1304.

Chivers, D. J., and C. M. Hladik. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. Journal of Morphology 166:337-386.
Clutton-Brock, T., and P. Harvey. 1977. Species differences in feeding and ranging behaviour in primates. In (T. Clutton-Brock, Ed.) Primate Ecology. London: Academic Press.
Conklin-Brittain, N. L., R. W. Wrangham, and K. D. Hunt. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. International Journal of Primatology 19:971-998.
Corlett, R., and P. Lucas. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). Oecologia 82:166-171.
Defler, T. R., and S. B. Defler. 1996. Diet of a group of *Lagothrix Lagothricha Lagothricha* in southeastern Colombia. International Journal of Primatology 17:161-190.
Dirzo, R., and P. H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137-167.
Duncan, R. S., and C. A. Chapman. 2002. Limitations of Animal Seed Dispersal for Enhancing Forest Succession on Degraded Lands. Pages 437-450 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing., Wallingford, U.K.
Dutton, P., and H. Chapman. 2015. Dietary preferences of a submontane population of the rare Nigerian-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Ngel Nyaki Forest Reserve, Nigeria. American journal of primatology 77:86-97.
Eckardt, W., and K. Zuberbühler. 2004. Cooperation and competition in two forest monkeys. Behavioral Ecology 15:400-411.
Effiom, E. O., G. Nuñez-Iturri, H. G. Smith, U. Ottosson, and O. Olsson. 2013. Bushmeat hunting changes regeneration of African rainforests. Proceedings of the Royal Society of London B: Biological Sciences 280:20130246.
Elmhagen, B., M. Tannerfeldt, and A. Angerbjörn. 2002. Food-niche overlap between arctic and red foxes. Canadian Journal of Zoology 80:1274-1285.
Else, J. G. 1991. Nonhuman primates as pests. Pages 155-165 Primate responses to environmental change. Springer, Netherlands.
Erhart, E. M., and D. J. Overdorff. 1999. Female coordination of group travel in wild Propithecus and Eulemur. International Journal of Primatology 20:927-940.
Fa, J. E., J. Juste, J. P. Val, and J. Castroviejo. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conservation biology 9:1107-1115.
Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics 34:487-515.
Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. Conservation biology 19:680-688.
Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, and H. K. Gibbs. 2005. Global consequences of land use. Science 309:570-574.
Forget, P.-M., A. Dennis, S. Mazer, P. Jansen, S. Kitamura, J. Lambert, and D. A. Westcott. 2007. Seed allometry and disperser assemblages in tropical rainforests: a comparison of four floras on different continents. 2007) Seed dispersal: theory and its application in a changing world. Wallingford, UK: CAB International Publishing:5-36.
Garber, P. 1987. Foraging strategies among living primates. Annual review of Anthropology 16:339-364.
Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. The Journal of Animal Ecology 49:237-269.
Gautier-Hion, A. 1988. The diet and dietary habits of forest guenons. Pages 257-283 A primate radiation: Evolutionary biology of the African guenons. Cambridge University Press, Cambridge.
Gautier-Hion, A., J.-M. Duplantier, R. Quris, F. Feer, C. Sourd, J.-P. Decoux, G. Dubost, L. Emmons, C. Erard, and P. Hecketsweiler. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65:324-337.

Gawaisa, S. 2006. How important are putty nosed monkeys (*Cercopithecus nicitans*) in montane forest seed dispersal? Federal University of Technology.

Gross-Camp, N. D., and B. A. Kaplin. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. Acta Oecologica **37**:578-586.

Gross-Camp, N., and B. A. Kaplin. 2005. Chimpanzee (*Pan troglodytes*) Seed Dispersal in an Afromontane Forest: Microhabitat Influences on the Postdispersal Fate of Large Seeds. Biotropica **37**:641-649.

Hanski, I. 2005. Landscape fragmentation, biodiversity loss and the societal response. EMBO reports **6**:388-392.

Hanya, G., M. Kiyono, A. Yamada, K. Suzuki, M. Furukawa, Y. Yoshida, and A. Chijiiwa. 2006. Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. Primates **47**:275-278.

Harrison, M. J. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Animal behaviour **31**:969-977.

Henrik Bruun, H., and P. Poschlod. 2006. Why are small seeds dispersed through animal guts: large numbers or seed size per se? Oikos **113**:402-411.

Hey, D. D. 1964. The control of vertebrate problem animals in the province of the Cape of Good Hope, Republic of South Africa.*in* Proceedings of the 2nd Vertebrate Pest Control Conference.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual review of ecology and systematics **13**:201-228.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. Journal of theoretical Biology **29**:151-154.

Ihuma, J. 2007. Dispersal failure in Afromontane riverine forest fragments as a consequence of forest fragmentation and degradation. . Federal University of Technology, Nigeria.

Jones, M. E., and L. A. Barmuta. 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. Journal of animal ecology **67**:410-421.

Kaplin, B., and T. Moermond. 2000. Foraging ecology of the mountain monkey (*Cercopithecus l'hoesti*): implications for its evolutionary history and use of disturbed forest. American journal of primatology **50**:227-246.

Kaplin, B., V. Munyaligoga, and T. Moermond. 1998a. The Influence of Temporal Changes in Fruit Availability on Diet Composition and Seed Handling in Blue Monkeys (*Cercopithecus mitis doggetti*). Biotropica **30**:56-71.

Kaplin, B. A., and J. E. Lambert. 2002. Effectiveness of Seed Dispersal by Cercopithecus Monkeys: Implications for Seed

Input into Degraded Areas.*in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, New York.

Kaplin, B. A., and T. C. Moermond. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. American journal of primatology **45**:83-101.

Kaplin, B. A., V. Munyaligoga, and T. C. Moermond. 1998b. The Influence of Temporal Changes in Fruit Availability on Diet Composition and Seed Handling in Blue Monkeys (Cercopithecus mitis doggetti). Biotropica **30**:56-71.

King, F., and P. Lee. 1987. A brief survey of human attitudes to a pest species of primate – *Cercopithecus aethiops*. Primate Conservation **8**:82-84.

Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1999. The importance of figs to Sulawesi's imperiled wildlife. Tropical Biodiversity **6**:5-18.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, and J. Pino. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology letters **13**:597-605.

Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and Strychnos mitis: evidence for plant benefits beyond seed dispersal. International Journal of Primatology **22**:189-201.

Lambert, J. E. 2010. Primate frugivory and seed dispersal: Implications for the conservation of biodiversity. Evolutionary Anthropology: Issues, News, and Reviews **19**:165-166.

Lambert, J. E., and P. A. Garber. 1998. Evolutionary and ecological implications of primate seed dispersal. American journal of primatology **45**:9-28.
Lawes, M. 1991. Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in the Cape Vidal dune forest, South Africa. Journal of Zoology **224**:149-173.
Lawes, M., S. Henzi, and M. Perrin. 1990. Diet and feeding behaviour of samango monkeys (Cercopithecus mitis labiatus) in Ngoye forest, South Africa. Folia Primatologica **54**:57-69.
Leca, J.-B., N. Gunst, B. Thierry, and O. Petit. 2003. Distributed leadership in semifree-ranging white-faced capuchin monkeys. Animal behaviour **66**:1045-1052.
Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia **52**:22-30.
Linton, L., R. W. Davies, and F. Wrona. 1981. Resource utilization indices: an assessment. The Journal of Animal Ecology:283-292.
Magurran, A. E. 2013. Measuring biological diversity. John Wiley & Sons.
Marshall, A. J., C. M. Boyko, K. L. Feilen, R. H. Boyko, and M. Leighton. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology **140**:603-614.
Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology **28**:1219-1235.
Matsuda, I., Y. Akiyama, A. Tuuga, H. Bernard, and M. Clauss. 2014. Daily feeding rhythm in proboscis monkeys: a preliminary comparison with other non-human primates. Primates **55**:313-326.
Matthews, L. J., C. Arnold, Z. Machanda, and C. L. Nunn. 2010. Primate extinction risk and historical patterns of speciation and extinction in relation to body mass. Proceedings of the Royal Society of London B: Biological Sciences:DOI: 10.1098/rspb.2010.1489.
McConkey, K. R., F. Aldy, A. Ario, and D. J. Chivers. 2002. Selection of fruit by gibbons (*Hylobates muelleri× agilis*) in the rain forests of central Borneo. International Journal of Primatology **23**:123-145.
McConkey, K. R., and W. Y. Brockelman. 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology **92**:1492-1502.
McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biological Conservation **146**:1-13.
Meijaard, E., D. Sheil, R. Nasi, D. Augeri, B. Rosenbaum, D. Iskandar, T. Setyawati, M. Lammertink, I. Rachmatika, A. Wong, T. Soehartono, S. Stanley, and T. O'Brien. 2005. Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo. CIFOR and UNESCO, Indonesia.
Milton, K. 1998. Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. International Journal of Primatology **19**:513-548.
Moberg, F., and P. Rönnbäck. 2003. Ecosystem services of the tropical seascape: interactions, substitutions and restoration. Ocean & Coastal Management **46**:27-46.
Mysterud, A. 2000. Diet overlap among ruminants in Fennoscandia. Oecologia **124**:130-137.
Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in ecology & evolution **15**:278-285.
Nishida, T. 2002. Competition between baboons and chimpanzees at Mahale. Pan Afrrican News **9**:23-26.
O'Brien, R. G., and M. K. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. Psychological bulletin **97**:316.
Oates, J. F., and C. P. Groves. 2008. *Cercopithecus nictitans*.
Oates, J. F., P. G. Waterman, and G. M. Choo. 1980. Food selection by the south Indian leaf-monkey, Presbytis johnii, in relation to leaf chemistry. Oecologia **45**:45-56.
Overdorff, D. J. 1996. Ecological correlates to activity and habitat use of two prosimian primates: Eulemur rubriventer and Eulemur fulvus rufus in Madagascar. American journal of primatology **40**:327-342.
Parrotta, J. A., J. W. Turnbull, and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**:1-7.
Peres, C. A. 1996. Food patch structure and plant resource partitioning in interspecific associations of Amazonian tamarins. International Journal of Primatology **17**:695-723.

Peres, C. A., and M. van Roosmalen. 2002. Primate frugivory in two species-rich neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford:407-421.
Phillips, R. B., C. S. Winchell, and R. H. Schmidt. 2007. Dietary overlap of an alien and native carnivore on San Clemente Island, California. Journal of Mammalogy 88:173-180.
Porter, L. M., C. C. Gilbert, and J. G. Fleagle. 2014. Diet and phylogeny in primate communities. International Journal of Primatology 35:1144-1163.
Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B: Biological Sciences 267:1947-1952.
Robinson, J. G. 1984. Diurnal variation in foraging and diet in the wedge-capped capuchin *Cebus olivaceus*. Folia Primatologica 43:216-228.
Rothman, J. M., C. A. Chapman, and P. J. Van Soest. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542-566.
Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.
Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.
Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Pages 15-29 Frugivory and seed dispersal: ecological and evolutionary aspects. Springer, Netherlands.
Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333-353.
Setchell, J. M., and D. J. Curtis. 2011. Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge.
Shannon, C. E., and W. Weaver. 1949. The mathematical theory of information.
Sorensen, T. C., and L. M. Fedigan. 2000. Distribution of three monkey species along a gradient of regenerating tropical dry forest. Biological Conservation 92:227-240.
Stevenson, P. R. 2004. Fruit choice by woolly monkeys in Tinigua National Park, Colombia. International Journal of Primatology 25:367-381.
Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. Oikos 58:239-250.
Thia, J. A. 2014. The plight of trees in disturbed forest: conservation of Montane Trees, Nigeria.
Tripathi, R., and M. Khan. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of Quercus in a subtropical wet hill forest. Oikos 57:289-296.
Tutin, C., R. Ham, and L. White. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American journal of primatology 42:1-24.
Tutin, C. E. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249-265.
Tweheyo, M., K. A. Lye, and R. B. Weladji. 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. Forest Ecology and Management 188:267-278.
Vander Wall, S. B., P.-M. Forget, J. E. Lambert, and P. E. Hulme. 2005. Seed fate pathways: filling the gap between parent and offspring. Pages 1-8 Seed fate: Predation, dispersal and seedling establishment. CABI Publishing, Wallingford, UK.
Vitousek, P. M., and R. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual review of ecology and systematics 17:137-167.
Wahungu, G. 1998. Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey Cercocebus galeritus and yellow baboon Papio cynocephalus. African Journal of Ecology 36:159-173.
Waterman, P. G., G. M. Choo, A. L. Vedder, and D. Watts. 1983. Digestibility, digestion-inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. Oecologia 60:244-249.
Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecological Monographs 70:331-351.
Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3:37-50.

Wheelwright, N. T. 1985. Fruit-Size, Gape Width, and the Diets of Fruit-Eating Birds. Ecology 66:808-818.
Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American naturalist 125:879-887.
Wrangham, R. W., C. A. Chapman, and L. J. Chapman. 1994. Seed dispersal by forest chimpanzees in Uganda. Journal of Tropical Ecology 10:355-368.
Wunderle Jr, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.
Zar, J. H. 1999. Biostatistical analysis. Pearson Education, India.
Zuidema, P. A., J. A. Sayer, and W. Dijkman. 1996. Forest fragmentation and biodiversity: the case for intermediate-sized conservation areas. Environmental conservation 23:290-297.

4| Potential fallback species in *C. nictitans* diet at Ngel Nyaki Forest Reserve, Nigeria.

Introduction

Most primate species live in environments with both spatial and temporal food heterogeneity, and as a consequence experience periods of extreme food scarcity. Such periods of scarcity are referred to as ecological crunches, bottlenecks or critical use periods (Marshall et al. 2009). Species or Food items that primates eat disproportionately to their availability are considered their 'preferred' foods. These foods are usually costly to produce, being high in energy and protein, and are therefore relatively uncommon (Marshall and Wrangham 2007). Due to their high cost of production relative to many other foods , during crunch times preferred foods may not be produced or may be produced at such low levels that harvesting them is not energy efficient. At such times primates switch to other foods commonly known as 'fallback' foods. These are foods of relatively poor nutrient quality but of high abundance, which increase in importance at times when preferred foods are scarce (Marshall and Wrangham 2007). To exploit these relatively low quality foods, some species of primate have specialised adaptations. For example, the harder tooth enamel found in *Lophocebus albigena* (grey-cheeked mangabeys) (Lambert et al. 2004), *Cercocebus atys* (sooty mangabeys) (McGraw et al. 2014) and in great apes (Constantino et al. 2009) allows them to perforate thick outer protection of fruit and seeds.

Marshall and Wrangham (2007) defined fallback foods as "foods whose use is negatively correlated with availability of preferred foods". Therefore to qualify as a fallback food, items must be of high importance in terms of percentage of energy intake or feeding time during crunch times, and be non-preferred; a food that is used in low quantities and is of low quality by definition it is *not* a fallback food. Similarly, if a high quality preferred food is used in small quantities it is not a fallback food.

Identifying fallback species is important for both primate conservation and managing forest regeneration (Marshall and Wrangham 2007, Constantino and Wright 2009, Marshall et al. 2009, Hanya and Chapman 2013), yet they are easy to miss because they are only used in times of scarcity. (McConkey et al. 2002, Marshall and Wrangham 2007). For example, the removal of fallback foods via selective logging may only become apparent during crunch times, yet when this happens it could have strong deleterious effects, even if preferred food species are unaffected (Marshall et al. 2009, Hardus et al. 2012). The quality and availability of fallback foods, rather than preferred foods may be the limiting factor of primate biomass (Hanya and Chapman 2013).

In this paper I investigate the potential role of eleven species as fallback food for *C. nictitans* living in Ngel Nyaki reserve in Nigeria. Species were selected based on previous work done on *C. nictitans* at Ngel Nyaki and on indications from the literature that *Ficus* species may an important food for a number of primate species (Milton 1980, Utami et al. 1997, Furuichi et al. 2001, Marshall and Leighton 2006).

Methods

Field Site

The study was conducted at Ngel Nyaki Forest Reserve, a submontane forest reserve located on the western escarpment of the Mambilla Plateau (7°30 N, 11°30 E), in Taraba State, Nigeria at elevations between 1400-1600 MAMSL. Ngel Nyaki is a moderately-large forest fragment of approximately 7 km^2 , surrounded by a number of smaller riparian fragments (Chapman and Chapman 2001). Mean monthly minimum and maximum temperatures for the wet and dry seasons are 26 and 13 ° C, and 23 and 16 ° C respectively. Mean annual rainfall is approximately 1,800mm, occurring predominantly between April and October (Nigerian Montane Forest Project Weather data) (Fig 1.). In addition to *C. nictitans,* the forest contains five other primate species *Papio anubis* (olive baboon), *C. mona* (mona monkey), *Chlorocebus tantalus* (tantalus monkey), *Colobus guereza occidentalis* (black and white colobus monkey) and *Pan troglodytes ellioti* (Nigerian Cameroon chimpanzee) (Chapman et al. 2004).

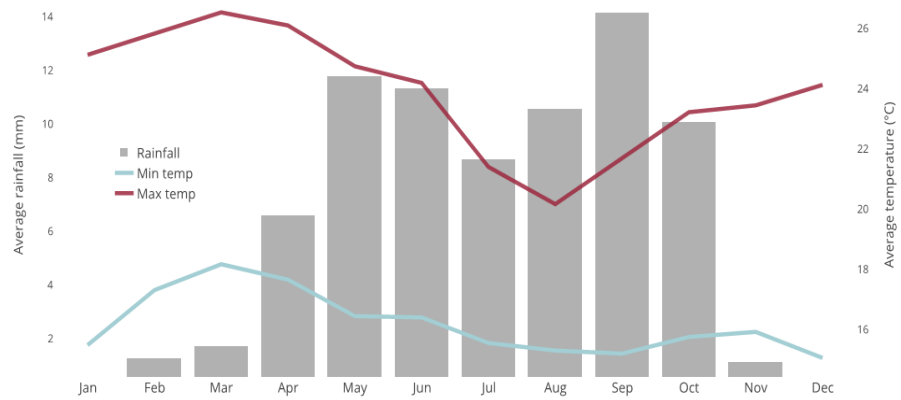


Fig 1. Mean daily rainfall (mm), minimum temperature (°c) and maximum temperature (°c) for each month at Ngel Nyaki reserve from January 2006 to March 2014.

Subjects

Behavioural observations were conducted over three years on three different *C. nictitans* troops. The first troop, SBT, was observed between January 2005 and December 2006 while the other two troops, BBT and MFT, were observed concurrently between October 2013 and October 2014. Due to the seven year gap between observations and low visibility making it difficult to identify individual monkeys, it was not possible to observe SBT in the 2013-2014 season.

SBT, which was not habituated, comprised 24 individuals and was considered representative of other troops in the area (Gawaisa 2006). Observations were conducted for eight hours a day (0600 to 1200 and 1600 to 1800), ten days per month over a two year period (January 2005 to December 2006). This resulted in 11,029 individual observations gathered over 240 days or 1920 hours. Data were collected by Stephen Gawaisa with the assistance of a local field assistant Musa Bawuro.

In the 2013 season observations were focused on two troops of semi-habituated *C. nictitans*, both living in the main forest. MFT comprised 19 individuals, including three sub-adults, one juvenile and two babies. BBT had 30 members, with one sub-adult and one baby. BBT was easily distinguished from MFT by its greater size but also because the individuals had larger body sizes compared with both MFT and all other *C. nictitans* troops

observed during 2013-2014. Additionally, incidental observations were made on other *C. nictitans* troops and individual males who were in the vicinity of the focal troops. Observing two troops allowed for a comparison among troops within a year, and provided a more representative sample of *C. nictitans* in the reserve. BBT and MFT demonstrated a notable degree of home range overlap with each other, as well as sharing at least part of their home range with other primate troops, including other *C. nictitans* troops. Observations were conducted over 487 days (October 2013 to February 2015) between dawn and dusk. This resulted in 109 hours and 30 minutes of observations. Data were collected by three observers in total, Musa Bawuro and myself from October 2013 through to February 2014, and Musa Bawuro and another field assistant, Thomas Patrick, from March 2014 to October 2014. There was a period of overlap in February in 2014 where all three observers worked concurrently to ensure inter-observer reliability.

Behavioural Data

Observations were conducted using scan sampling (Altmann 1974). In 2005 and 2006 scans were conducted for 15 minutes on the hour. The troop was systemically scanned from left to right on the first scan then right to left on the next, and so on. During these scans only one activity was recorded for each member. Scans were conducted from at least 50 m away and a telescope was used to help identify food items (Gawaisa 2006). As the length of scan increases, so does the likelihood that all individuals will be sampled. Longer inter-observation lengths also ensures that each sample is independent of the previous one, however it does decrease the likelihood that rare behaviours will be sampled within a given time period due to fewer observations creating a relatively smaller sample size (Martin and Bateson 1986).

During the 2013-2014 season scans of all visible members of the troop were conducted for one minute at 15 minute intervals. One minute was adequate to scan all visible members of the group and minimised the risk of double scoring the same individual in each scan. Scans were conducted using binoculars at distances of approximately 20 to 50 m to minimise disturbance to the troop that could alter their behaviour

Records were made of the individual's activity or state and of the details of the food item consumed. In 2005 and 2006, records were made of all items ingested, however during 2013-2014 food items were categorised

into six categories: fruit, new leaves, old leaves, flowers, insects or other. Items that constituted less than 5% of the diet in 2005-2006 were categorised as 'other' (stem, bark, fungi, tendrils, honey juice), new leaf (leaf buds) or flowers (orchids, flower buds). As not all insects were able to be identified they were grouped as one category. Difficulty differentiating ripe and unripe fruits, and mature and new leaves resulted in them being grouped in most analyses. As individual identity was not discernible, age, and for adult *C. nictitans,* sex, was recorded. Individuals were placed in one of five classes; adult female, adult male, sub-adult, juvenile and infant, with membership in a class being determined by size.

Phenology

Previous work demonstrated that Ngel Nyaki undergoes fluctuations in the availability of new leaves, immature and mature fruit (see Chapter 2) which results in periods of relative availability and scarcity. There were significantly less food species available in 2013-2014 than 2005 or 2006. The difference in availability was greater in species constituting *C. nictitans* diet than for species overall. In particular there was a notable decrease in fruit species available, a key and often preferred food item in primate diet (Irwin et al. 2015) (Fig 2). Based on the low availability compared to the both other years of observation, as well as from average availability between 2005 to 2014, 2013-2014 was identified as a potential crunch time, where we expected to see the use of fallback foods. In contrast, 2005 and 2006 were identified as years of average availability where *C. nictitans* would be more able to eat foods they preferred.

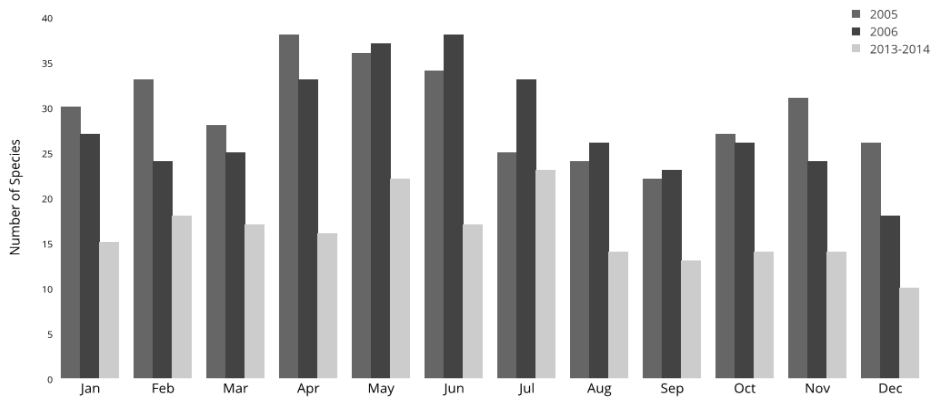


Fig 2. Monthly availability of species bearing fruit along transects in Ngel Nyaki forest. Species were scored a 'one' in any month where any tree along the phenology transect was observed with any amount of mature fruit during weekly observations. If fruit was observed that month the species was scored zero. Scores were then summed.

Preference

Food species that *C. nictitans* demonstrated preference for were determined in earlier work (see Chapter 3). It was found that in 2005 and 2006 *C. nictitans* showed preference for a total of six species; *Croton macrostachyus, Eugenia gilgii, Lannea barteri, Pterygota mildbraedii, Rauvolfia vomitoria and Symphonia globulifera. The availability of these foods in the wet and dry seasons were summed individually for use in analysis. Availability was calculated using trees found along established phenology transects. For each of the six species, n*ew leaves, flower buds, flowers, immature fruit and mature fruit were scored on a five point scale representing their percentage of crown coverage. A score of '0' indicated complete absence, '1' coverage up to 25%, '2' 25 to 50%, '3' 50 to 75% and '4' 75 to 100% (Sun ….2003?) As trees vary in size an analogue of abundance was then calculated by multiplying this score and the basal area of individual trees. This is not a measure of true abundance but is an estimate from the relationship between basal area and crown size, and the relationship of scores to percentage crown coverage (Setchell and Curtis 2011). It can therefore be used to compare relative abundance of food items and food availability between different time periods (REF). Using the phenological records to calculate relative abundance allowed for a consistent measure of food availability for both the historical 2005-2006 data and the recent 2013-2014 data.

	Year		
Species	2005	2006	2013
Albizia gummifera	1.34	0.16	0.47
Anthonotha noldeae	9.14	12.01	10.98
Beilschmiedia mannii	-	-	1.03
Celtis gomphophylla	7.02	12.78	6.19
Chrysophyllum albidum	0.28	0.68	0.40
Cordia millenii	-	-	0.02
Croton macrostachyus	0.71	-	-
Deinbollia sp.	0.12	1.89	1.13
Entandrophragma angolense	0.08	-	0.03
Eugenia gilgii	0.07	-	-
Ficus spp.	40.14	26.24	37.65
Isolona deightonii	5.27	6.20	0.01
Landolphia buchananii	4.11	-	0.39
Lannea barteri	0.46	0.23	-
Memecylon afzelii	-	0.07	-
Newtonia buchananii	0.29	0.30	0.08
Parkia filicoidea	1.15	1.54	3.64
Polyscias fulva	1.15	1.42	2.80
Pouteria altissima	12.82	16.12	34.46
Pterygota mildbraedii	0.98	0.44	-
Rauvolfia vomitoria	0.53	-	-
Rothmannia urcelliformis	0.40	0.30	-
Santiria trimera	3.43	7.77	0.96
Schefflera abyssinica	0.21	0.07	-
Syzygium guineense	2.46	1.17	1.40
Symphonia globulifera	1.43	0.16	0.01
Syzygium guineense	0.05	-	-
Tabernaemontana contorta	0.36	-	-
Trichilia welwitschii	3.18	1.98	-
Trilepisium madagascariense	0.03	0.44	0.08
Uapaca sp.	0.03	-	-
Unknown	2.84	3.17	0.19

Table 1. Proportion of independent feeding observations for each year on each of the 32 species identified species in *C. nictitans* diet across the three years of observation. Species highlighted grey were preferred species in one or more of the years.

Fallback species

Based on the findings from previous work (REF) previous work, I identified three species and one genus as potential fallback foods. The three species, *Parkia filicoidea, Polyscias fulva* and *Pouteria altissima* were selected as they showed both highest use and correspondingly lowest availability in 2013-2014 relative to the other two years? The genus *Ficus*, was included as it has been reported to be very important in a number of primate diets (Milton 1980, Utami et al. 1997, Furuichi et al. 2001, Marshall and Leighton 2006), including as a potential fallback species for *P. t. ellioti* in Ngel Nyaki forest (Dutton and Chapman 2015). Due to morphological similarities it was not possible to identify individual *Ficus* species. For simplicity, henceforth *Ficus spp.* will be referred to as a species.

For each identified species, three correlations were performed against the availability of preferred species using the cor.test function in R: 1) the percentage of independent feeding observations on all food types for that species in the wet and dry season, 2) percentage of observations of feeding on its fruits in the wet and dry season and 3) percentage of observations of feeding on its leaves in the wet and dry seasons. Fallback species would be expected to show a significant negative correlation of their use with the abundance of preferred foods. Fruits and leaves were considered separately from total consumption, as due to their different nutrient content it is probable that only part a species would be utilised as a fallback food (e.g. only leaves) (Marshall et al. 2009).

	Reason Included			
Species	High use 2013-2014	Preference 2013-2014	Use only 2013-2014	Literature
Ficus spp. **	X	X		X
Polyscias fulva **	X	X		
Pouteria altissima **	X	X		
Parkia filicoidea **			X	

Table 2. Criteria for consideration use as a potential fallback food in 2013-2014 by *C. nictitans* living in Ngel Nyaki reserve. High use was defined as contributing more than 1% to the total diet (placing species in the top 50% of consumed species). Preference was demonstrated in previous work (see Chapter 3) and was defined as a positive score greater than 0.4.

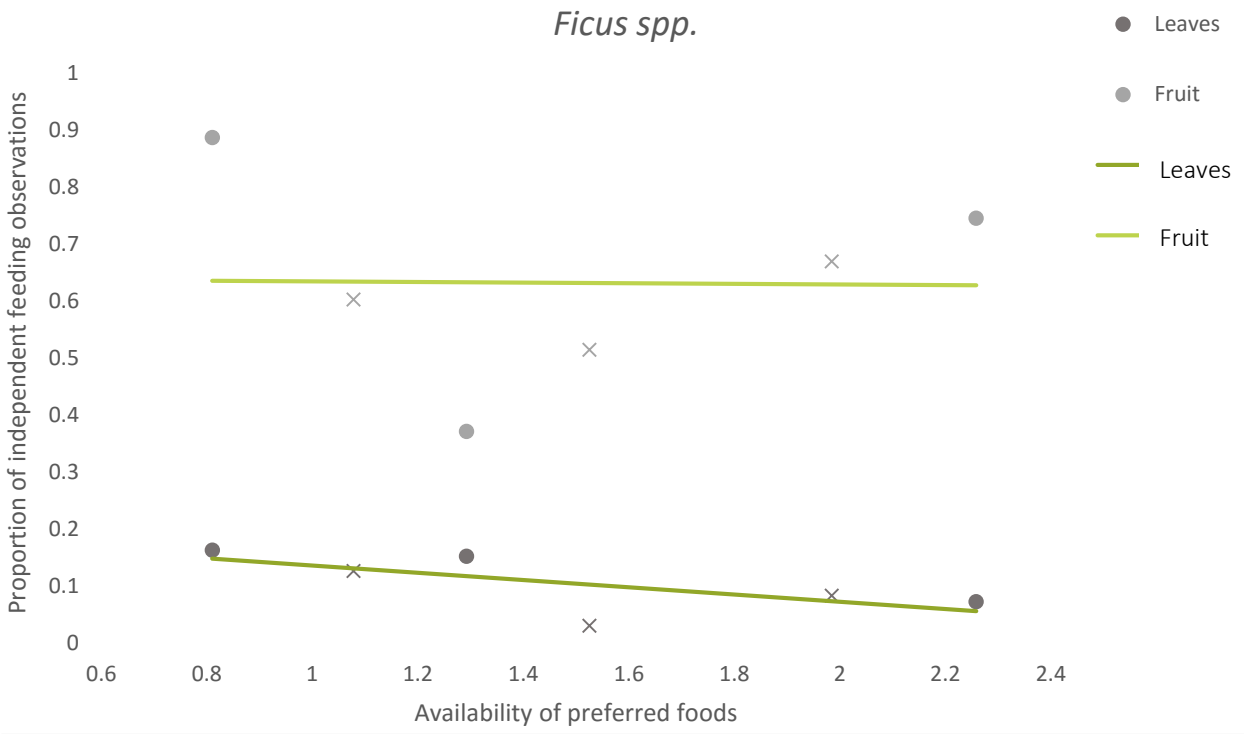
Results

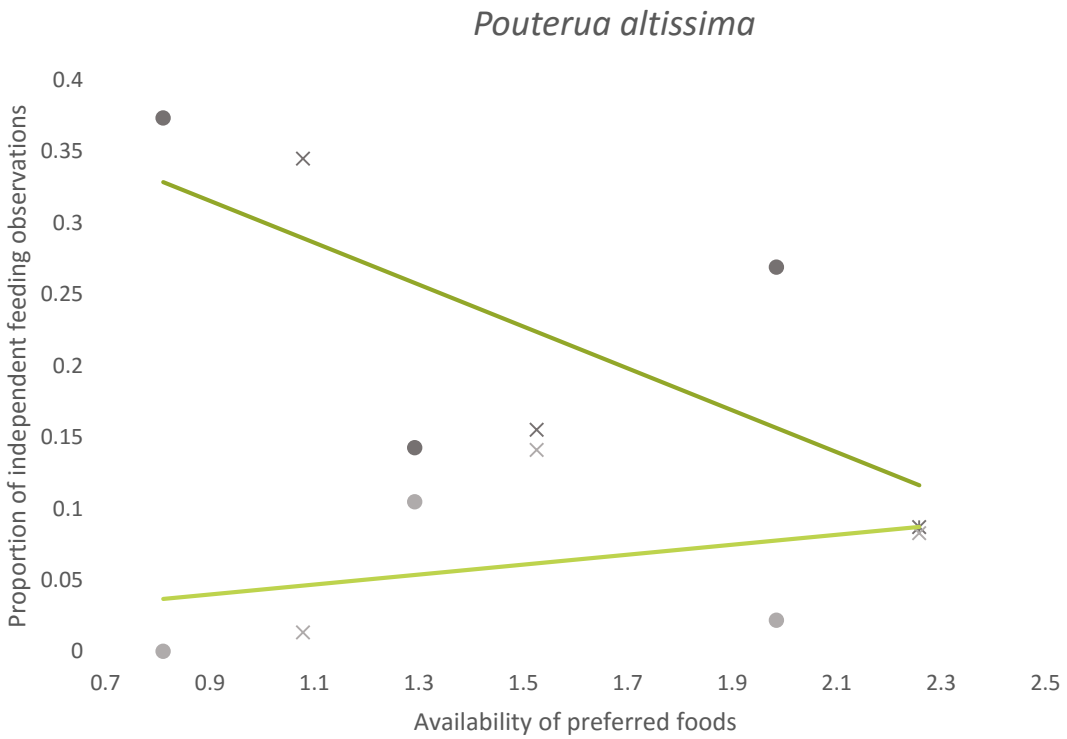
Fallback species

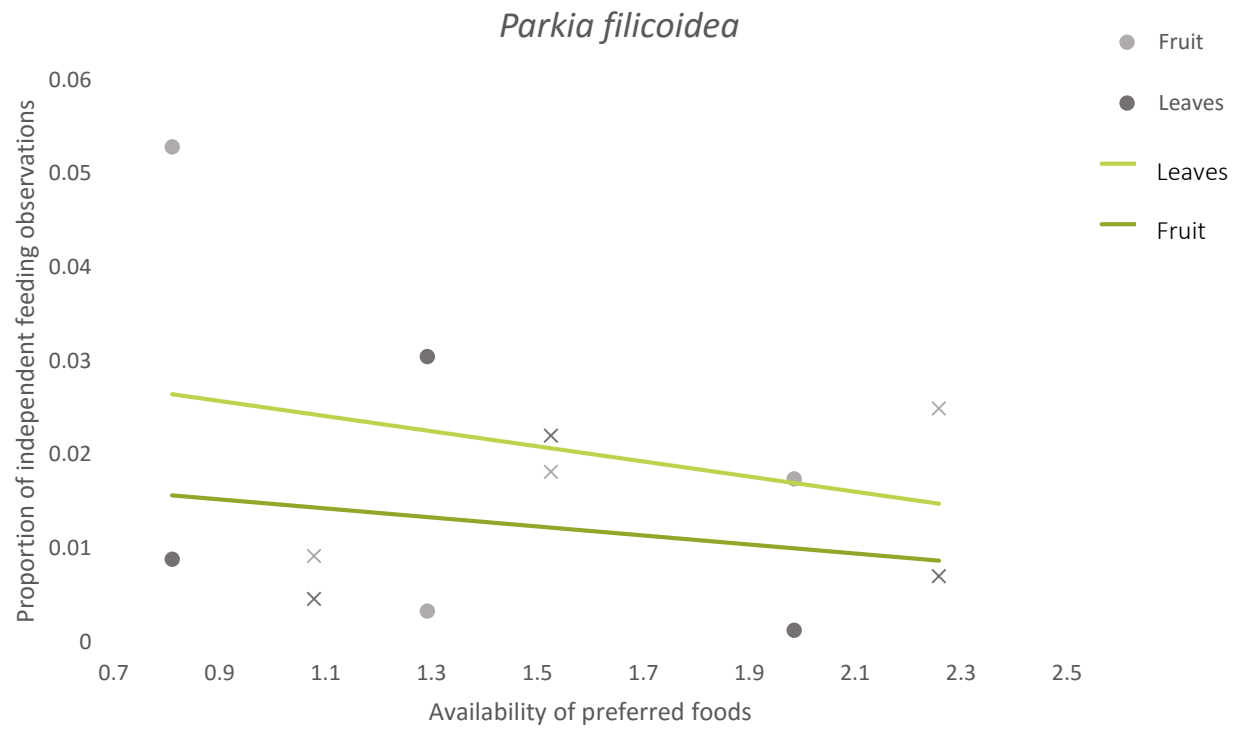
None of the twelve species showed a significant negative correlation of use with availability of food types; both total availability and availability of fruit and leaves only (Table 3); the strongest negative relationships were for *P. altissima* (r(4) = -0.6848, p = 0.1333), *Ficus spp.* (r(4) = -0.6815, p = 0.1360) and *Polyscias fulva* (r(4) = -0.6519, p = 0.1607) leaves (Fig 4). A significant strong positive relationship (r(4) = 0.9797, $p < 0.001$) with total availability and food use of *Ficus* spp suggest that Ficus it is unlikely to be a fallback food for *C. nictitans*. Likewise *P. altissima* fruit showed a moderate positive, but non-significant correlation (r(4) = 0.3350, $p = 0.5162$) with availability of preferred fruits.

	Species							
	Ficus spp.		*Pouteria altissima*		*Polyscias fulva*		*Parkia filicoidea*	
	r	*p*	r	*p*	r	*p*	r	*p*
Total	0.9797	<0.001*	-0.5467	0.2616	-0.2089	0.6912	-0.4074	0.4227
Fruit	-0.0168	0.9748	0.3350	0.5162	-0.3149	0.5433	-0.2556	0.6249
Leaves	-0.6815	0.1360	-0.6848	0.1333	-0.6519	0.1607	-0.2324	0.4227

Table 3. Results for Pearson's correlations of availability of food preferred by *C. nictitans* at Ngel Nyaki Forest Reserve with the proportion of independent feeding observations on the four species, *P. filicoidea, P. fulva, P. altissima* and *Ficus spp.* For each species proportional use of all food types (fruit, flowers, leaves), use of fruit, and use of leaves was correlated against preferred availability. Cells shaded grey indicate a positive correlation and an asterisks "*" is used to denote significance.


Ficus spp.
Leaves
Fruit
Leaves
Fruit
Proportion of independent feeding observations
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
Availability of preferred foods


Pouterua altissima
Proportion of independent feeding observations
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0.7
0.9
1.1
1.3
1.5
1.7
1.9
2.1
2.3
2.5
Availability of preferred foods



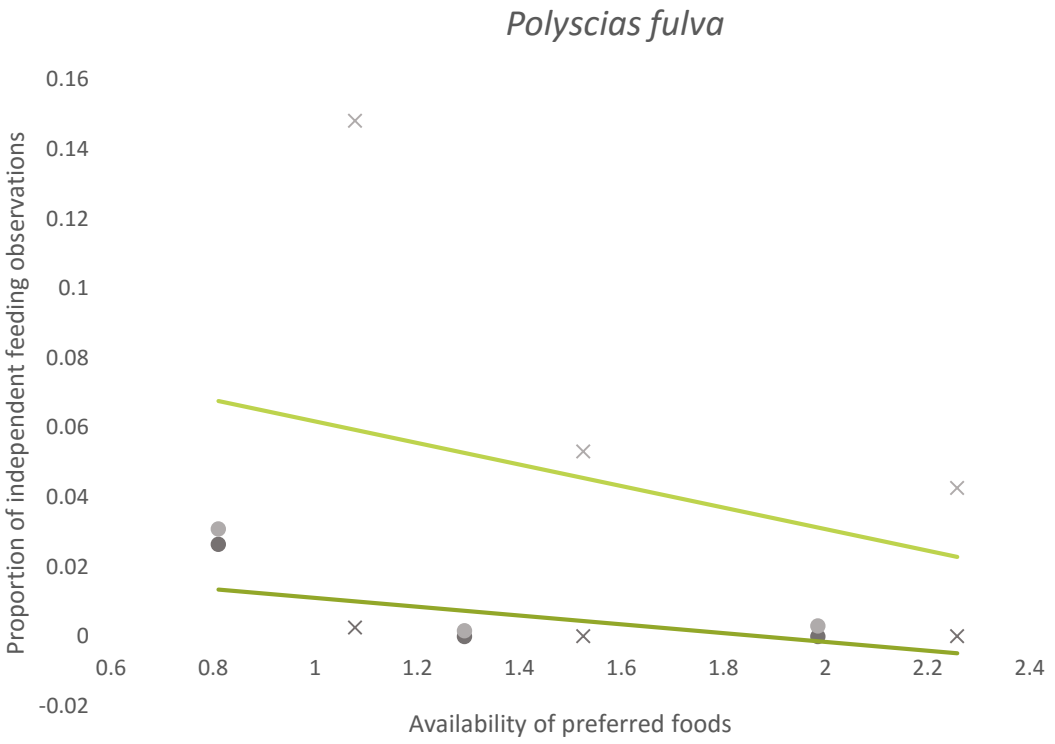


Fig 4. Pearson's correlations of availability of food preferred by *C. nictitans* at Ngel Nyaki with proportion of independent feeding observations on leaves and fruit of four species *P. filicoidea, P. fulva, P. altissima* and *Ficus spp.* Availability of preferred foods is an analogue of proportional crown coverage with a maximum value of four and is averaged over the species. All correlations are non-significant.

Discussion

In this study I investigated the potential for three tree species and one genus in Ngel Nyaki forest to act as fallback foods in the diet of *C. nictitans.* I found no statistically significant patters of food use suggestive of fallback foods, but three food species, *Pouteria altissima, Polyscias fulva* and *Ficus spp.* did show non significant trends indicative of fallback food behaviour. These species and others, warrant farther investigation with a larger data set; my study only looked at diet over six seasons and concentrated exclusively on tree species.

Consideration should be given to fallback species when making planting decisions when reforesting or rehabilitating degraded landscape, with the aim of attracting or better supporting primate populations (Marshall et al. 2009). Traditionally management plans have assumed that planting preferred species would be the optimal way to increase the carrying capacity of a habitat (Meijaard et al. 2005), however if fallback species even partially determine primate biomass this would not be the case (Marshall and Wrangham 2007). Planting fallbacks foods instead may maximise populations by providing them with more accessible food supplies in times of scarcity, reducing pressure on the population. This may have the additional benefit of reducing conflict with other primate species by reducing competition for overlapping preferred food, as well as with humans if it reduces the amount of crop raiding (Pienkowski et al. 1998).

It is possible that the non-significance of the trends can be explained by outliers distorting the analysis. Figure 5 describes the relationship between availability of preferred foods and consumption of the leaves of two potential fallback foods *P. altissima* and *Ficus spp..* Each point represents a season within the study. For both species one of the six points appears to exert disproportionate leverage, potentially causing the insignificant result in the trend (Zar 1999). It seems plausible that these points are the result of high (*P. altissima) or* low (*Ficus spp.*) values respectively at the start or end of a season. The wet and dry seasons are subject to yearly variations in actual duration, however, for the data analysis this was not taken into consideration. Rather, defined boundaries calculated from average data were imposed: (wet season = March to September and dry season = October to February, inclusive) (Wolda 1978, Nicholson 1994, Liebmann and Marengo 2001). This

could potentially be rectified if data were analysed in terms of monthly (rather than seasonal) use and availability, but this was not possible for this study due to the low number of feeding observation in the 2013-2014 wet season necessitating the pooling of data (Zar 1999). A more extreme case of this reasoning is illustrated by *P. fulva,* where the leaves were eaten only in 2013-2014 and only in very low quantities (Table 1). Such results lead to a correlation between two positive data points and four zeroes. Though these two data points do follow the expected trend, as above, more data collected within each month or data from more years would be needed before it was possible to determine if there was a statistically significant

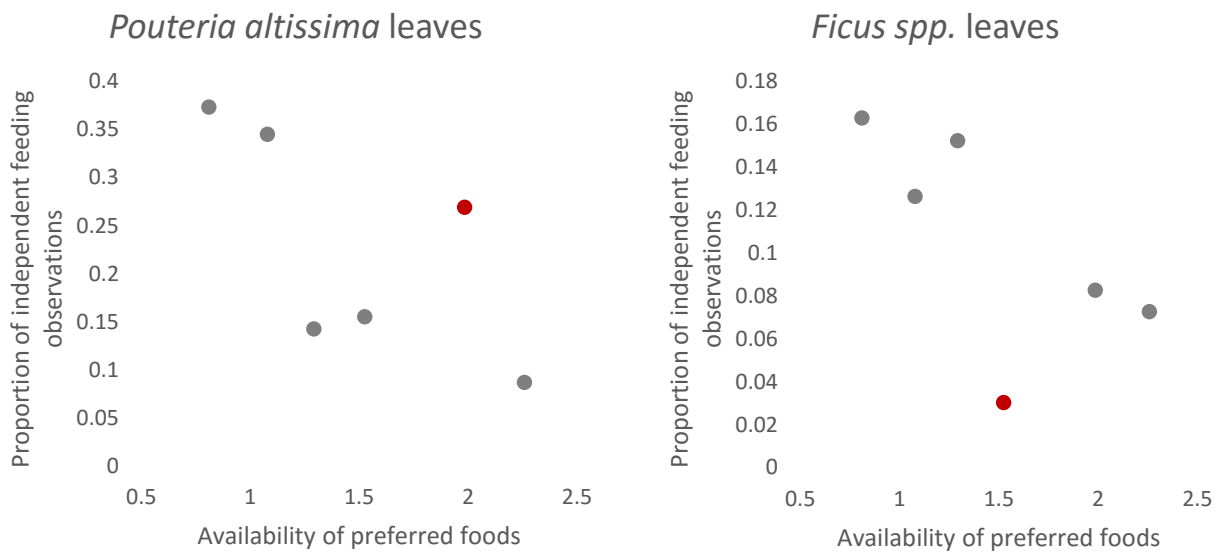


Fig 5. Availability of food preferred by *C. nictitans* at Ngel Nyaki plotted against the proportion of independent feeding observations on leaves of *Pouteria alitissma* and *Ficus spp.*. Availability of preferred foods is an analogue of proportional crown coverage with a maximum value of four and is averaged over the species. For each species one point with potentially high leverage has been highlighted in red.

Two food types, total use of *Ficus spp.* and *P. altissima* fruit showed a positive correlation with the availability of preferred food. In the case of *Ficus spp.* this was a strong statistically significant correlation. These results contradict the findings of Dutton and Chapman (2015) who found that *Ficus* fruit was a preferred food for *P. t. ellioti* at Ngel Nyaki, even when scarce. As well as the importance of *Ficus spp.* in the diet of many primate species (Milton 1980, Utami et al. 1997, Furuichi et al. 2001, Marshall and Leighton 2006). Increased intra-

specific competition for a scarce, highly valued resource may explain the positive relationship observed for *C. nictitans Ficus spp.* consumption with preferred food availability. If this was the case though not acting as a fallback food currently, its importance may increase upon the loss of *P. t. ellioti* from Ngel Nyaki. Low population numbers indicate that this may be a reality in the not too distant future (Knight 2014).

Though the relationship was significant, the relationship between availability of preferred foods and use of *Ficus spp.* (fig 4) in both the wet and dry season is v-shaped, with highest use and availability in 2005, high use and lowest availability in 2013-2014 and lowest use and moderate availability in 2006. This is potentially and artefact of treating a genus as a species. At Ngel Nyaki informal observations indicate *C. nictitans* only consume certain *Ficus sp.* e.g *Ficus lutea* and avoid other completely e.g, *Ficus sur.* All analysis, including that for preference, grouped both these 'liked' and 'disliked' together averaging the effect. If individual *Ficus spp.* were analysed it is possible that some species may be classified as 'preferred'. Of all years of observation 2005 had greatest total availability (See Chapter 2), it would be expected that *C. nictitans* would seek out and consume these 'preferred' *Ficus sp.* resulting in high *Ficus spp.* consumption. In 2006 and 2013-2014, which had lower overall availability, 'preferred' *Ficus spp.* may be rare due to the cost to produce them. Other less nutritious species may however still be available and experience increased use with scarcity i.e. be fallback foods. It was beyond the scope of this study to identify individual *Ficus sp.* however so it is not currently possible to determine if this is the case.

Another possibility for this V-shape, is that high inter-specific competition lowered *Ficus spp.* consumption in 2006 and that as the correlation suggests the relationship between *Ficus spp.* use and availability of preferred foods is positive. Previous work showed that for *C. nictitans* a decrease in availability can be greater than consideration of all species would indicate (See Chapter 2). It is reasonable to assume this would also be true for other primate species. It may be that during this period another species, such as *P. t. ellioti* was experiencing a decrease in availability of preferred food, causing it to rely on fallback foods. This would increase inter-specific completion for *Ficus spp.* a known fallback food for *P. t. ellioti*, which due to the smaller size of *C. nictitans* would most likely result in them decreasing *Ficus spp.* consumption (Mitani 1991,

Stevenson et al. 2000). Better understanding of community-level dynamics of the feeding ecology of primates at Ngel Nyaki would help better identify important plant species interactions, as these are most likely complex and involving multiple species of flora and fauna (Poulsen et al. 2002). As mentioned above, having data analysed monthly not seasonally would lower the leverage of each individual point potentially changing observed trends. However this was not possible with current data.

This positive correlation is also at odds with the observed negative correlation between availability of preferred and use of *Ficus spp.* leaves. *Ficus spp.* leaves were identified as a potential fallback food as observed non-significance was likely due to small sample size. This disparity, with increased use of a part with concurrent decreased use of whole species with scarcity, highlights the importance of investigation separate edible components of a food species and not the whole plant (Thomas and Taylor 1990)..

Though no significant relationship was found it seems premature to say that *C. nictitans* lacks a fallback food, partially due to these statistical quirks but also due to the limited scope of the investigation.

Other species

The fact that I only showed trends, rather than significant relationship fbetween choice and species and/or food type may reflect my choice of woody plants. My focus was on woody species because these are the ones that are included in the regular phenology transects at Ngel Nyaki, Moreover , it is important when studying fallback foods to consider more than a 12 to 24 month period (McConkey et al. 2002, Marshall and Wrangham 2007). Other studies haveobserved primates using lichens (Grueter et al. 2009), exudates (Porter et al. 2009), seeds (Hanya and Bernard 2012) and lianas (Dunn et al. 2012) as full back foods. Unfortunately, study design meant that these food types could not be more fully investigated in this study. The uses of lichens and exudates was not formally tracked, however the decrease in use of 'other' food types (which these foods would be included in) in 2013-2014 compared to 2005 and 2006 makes it seem unlikely that they are fallback foods. The consumption of immature fruit as a form of seed predation (Janzen 1971) was not differentiated in 2005 and 2006 from consumption of mature fruits, disallowing investigation of seeds as a fallback food, however informal observations of a low spitting rate in 2013-2014 by the author indicates this

may be a fruitful avenue to explore. Lianas were removed from analysis as many are unidentified, and none are tracked for availability along phenology transects. This meant that in the historical data (2005 and 2006) it was unclear if consumption on unidentified items was on lianas or some other food species, and that we were unable to determine if increased use was the result of a one- off increase in availability and neutral selection or due to being a fallback food for *C. nictitans.* In future it would be worthwhile to explore this, either by including liana consumption systematically in studies or as part of a focused study.

In terms of changes in proportional diet composition, arthropods may be a candidate for fallback foods in *C. nictitans* and excluding them from the analysis may have resulted in failing to find a fallback food. Though an uncommon food item in 2005 and 2006, there was a dramatic increase in their utilisation by both male and female *C. nictitans* in 2013-2014 . I excluded arthropods from this analysis due to the imprecise nature under which the arthropod data were collected; I did not know the relative availability of arthropods in each year. To fully understand the role of arthropods would need careful observation of the fruits on trees which *C. nictitans* were observed consuming from or determining the relative presence of arthropod remains in faecal matter between years (Deblauwe 2009, Mosdossy et al. 2015). Both these methods would warrant a dedicated study, beyond the scope of this preliminary investigation. The large increase in low fruit production years, in contrast to studies of *C. nictitans* diets in Gabon (Tutin et al. 1997, Tutin 1999, Brugiere et al. 2002) and Cameroon (Poulsen et al. 2002) definitely warrants more thorough examination.

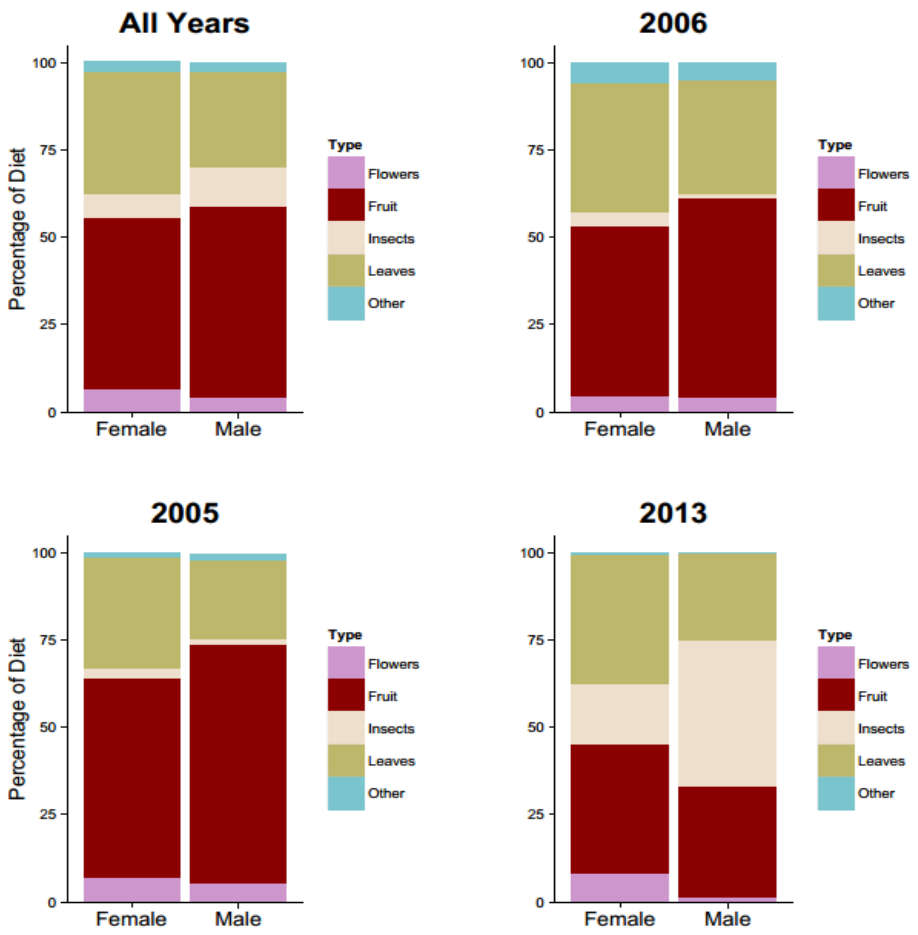


Fig 3. Proportional consumption of five food types (flowers, fruit, arthropods/insects, leaves, other) by adult female and male *C. nictitans* in 2005, 2006, 2013-2014 (2013 in figure) and for the average of 2005, 2006 and 2013-2014. Each food type combines all stages of maturity for that food type.

Fallback habitats

The inability of my study to identify any fallback species may have also been the result of considering each species individually. Instead of relying on particular species as fallback food *C. nictitans* may instead be utilising fallback habitats, which due to their ecological factors may have a high number of *P. fulva, P. altissima* and *Ficus spp.* (Marshall et al. 2009). These species or habitats may also be conducive to supporting a high arthropod biomass, fitting with the potential importance of their role in *C. nictitans* diet in times of scarcity. If this was the case it may be that each species individually does not demonstrate a statistical correlation, rather the use of the fallback habitat is negatively correlated with use of more preferable habitat (Marshall et al. 2009). This may be indicated by a change in home range in times of scarcity or through careful analysis of

habitats within the forest and differential use by *C. nictitans* of these (Dunn et al. 2012). Though the home range of the 2013-2014 troops is known, that of the troop from 2005 and to 2006 is not, so this remains beyond the scope of this study, however the 2013-2014 data could be used in conjunction with data from other years of average or high availability.

Furthermore, as this was only a preliminary investigation, a number of potential possibilities were not explored, including non-woody food types and the potential for fallback habitats. *C. nictitans* shows clear, significant changes in its diet during crunch times, these may influence its role as seed disperser. Therefore it is imperative that we understand which food it uses in times of scarcity so that this information can be factored into conservation management plans.

Conclusion

I found no conclusive evidence that any one food type served as a fallback food for *C. nictitans* living in Ngel Nyaki forest. However three tree species showed indications that *C. nictitans* may use their leaves as a fallback food: *Polysicias fulva, Pouteria altissima* and *Ficus spp..* These species, as well as the role of lianas and arthropods in *C. nictitans* diet warrant further investigation. . Future studies should investigate the possibility that some or all of these species form a fallback habitatDoing so will allow for informed, precise and targeted conservation recommendations which may assist in both primate conservation as well as forest regeneration and rehabilitation plans.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour **49**:227-266.

Brugiere, D., J.-P. Gautier, A. Moungazi, and A. Gautier-Hion. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology **23**:999-1024.

Chapman, H. M., S. M. Olson, and D. Trumm. 2004. An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. Oryx **38**:282-290.

Chapman, J., and H. Chapman. 2001. The Forests of Taraba and Adamawa States, Nigeria. *An Ecological Account and Plant Species Checklist*. University of Canterbury, New Zealand.

Constantino, P. J., P. W. Lucas, J. J. W. Lee, and B. R. Lawn. 2009. The influence of fallback foods on great ape tooth enamel. American Journal of Physical Anthropology **140**:653-660.

Constantino, P. J., and B. W. Wright. 2009. The importance of fallback foods in primate ecology and evolution. American Journal of Physical Anthropology **140**:599-602.

Deblauwe, I. 2009. Temporal variation in insect-eating by chimpanzees and gorillas in southeast Cameroon: extension of niche differentiation. International Journal of Primatology **30**:229-252.

Dunn, J. C., N. Asensio, V. Arroyo-Rodríguez, S. Schnitzer, and J. Cristóbal-Azkarate. 2012. The ranging costs of a fallback food: liana consumption supplements diet but increases foraging effort in howler monkeys. Biotropica **44**:705-714.

Dutton, P., and H. Chapman. 2015. Dietary preferences of a submontane population of the rare Nigerian-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Ngel Nyaki Forest Reserve, Nigeria. American journal of primatology **77**:86-97.

Furuichi, T., C. Hashimoto, and Y. Tashiro. 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. International Journal of Primatology **22**:929-945.

Gawaisa, S. 2006. How important are putty nosed monkeys (*Cercopithecus nicitans*) in montane forest seed dispersal? Federal University of Technology.

Grueter, C. C., D. Li, B. Ren, F. Wei, Z. Xiang, and C. P. van Schaik. 2009. Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. American Journal of Physical Anthropology **140**:700-715.

Hanya, G., and H. Bernard. 2012. Fallback foods of red leaf monkeys (Presbytis rubicunda) in Danum Valley, Borneo. International Journal of Primatology **33**:322-337.

Hanya, G., and C. A. Chapman. 2013. Linking feeding ecology and population abundance: a review of food resource limitation on primates. Ecological research **28**:183-190.

Hardus, M. E., A. R. Lameira, S. B. Menken, and S. A. Wich. 2012. Effects of logging on orangutan behavior. Biological Conservation **146**:177-187.

Irwin, M. T., J.-L. Raharison, D. R. Raubenheimer, C. A. Chapman, and J. M. Rothman. 2015. The Nutritional Geometry of Resource Scarcity: Effects of Lean Seasons and Habitat Disturbance on Nutrient Intakes and Balancing in Wild Sifakas. PloS one **10**:DOI:10.1371/journal.pone.0128046.

Janzen, D. H. 1971. Seed predation by animals. Annual review of ecology and systematics:465-492.

Knight, A. 2014. The genetic structure and dispersal patterns of the Nigeria-Cameroon Chimpanzee (Pan troglodytes ellioti).

Lambert, J. E., C. A. Chapman, R. W. Wrangham, and N. L. Conklin-Brittain. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. American Journal of Physical Anthropology **125**:363-368.

Liebmann, B., and J. Marengo. 2001. Interannual variability of the rainy season and rainfall in the Brazilian Amazon Basin. Journal of Climate **14**:4308-4318.

Marshall, A. J., C. M. Boyko, K. L. Feilen, R. H. Boyko, and M. Leighton. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology **140**:603-614.

Marshall, A. J., and M. Leighton. 2006. How does food availability limit the population density of white-bearded gibbons? Feeding ecology in apes and other primates **48**:313.
Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology **28**:1219-1235.
Martin, P., and P. Bateson. 1986. Measuring behavior. Cambridge Univ. Press, Cambridge.
McConkey, K. R., F. Aldy, A. Ario, and D. J. Chivers. 2002. Selection of fruit by gibbons (*Hylobates muelleri× agilis*) in the rain forests of central Borneo. International Journal of Primatology **23**:123-145.
McGraw, W. S., A. E. Vick, and D. J. Daegling. 2014. Dietary variation and food hardness in sooty mangabeys (Cercocebus atys): Implications for fallback foods and dental adaptation. American Journal of Physical Anthropology **154**:413-423.
Meijaard, E., D. Sheil, R. Nasi, D. Augeri, B. Rosenbaum, D. Iskandar, T. Setyawati, M. Lammertink, I. Rachmatika, A. Wong, T. Soehartono, S. Stanley, and T. O'Brien. 2005. Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo. CIFOR and UNESCO, Indonesia.
Milton, K. 1980. The foraging strategy of howler monkeys: a study in primate economics. Columbia University Press.
Mitani, M. 1991. Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. Primates **32**:137-151.
Mosdossy, K. N., A. D. Melin, and L. M. Fedigan. 2015. Quantifying seasonal fallback on invertebrates, pith, and bromeliad leaves by white-faced capuchin monkeys (Cebus capucinus) in a tropical dry forest. American Journal of Physical Anthropology.
Nicholson, S. E. 1994. Recent rainfall fluctuations in Africa and their relationship to past conditions over the continent. The Holocene **4**:121-131.
Pienkowski, M., A. Watkinson, G. Kerby, L. NAUGHTON-TREVES, A. TREVES, C. CHAPMAN, and R. WRANGHAM. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. Journal of Applied Ecology **35**:596-606.
Porter, L. M., P. A. Garber, and E. Nacimento. 2009. Exudates as a fallback food for Callimico goeldii. American journal of primatology **71**:120-129.
Poulsen, J. R., C. J. Clark, E. F. Connor, and T. B. Smith. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. Ecology **83**:228-240.
Setchell, J. M., and D. J. Curtis. 2011. Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge.
Stevenson, P. R., M. J. Quiñones, and J. A. Ahumada. 2000. Influence of Fruit Availability on Ecological Overlap among Four Neotropical Primates at Tinigua National Park, Colombia1. Biotropica **32**:533-544.
Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. The Journal of wildlife management:322-330.
Tutin, C., R. Ham, and L. White. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American journal of primatology **42**:1-24.
Tutin, C. E. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates **40**:249-265.
Utami, S. S., S. A. Wich, E. H. Sterck, and J. A. van Hooff. 1997. Food competition between wild orangutans in large fig trees. International Journal of Primatology **18**:909-927.
Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. The Journal of Animal Ecology:369-381.
Zar, J. H. 1999. Biostatistical analysis. Pearson Education, India.

Conclusion

The current study demonstrated that like other guenons, *Cercopithecus nictitans* living in Ngel Nyaki Forest Reserve have a high degree of ecological flexibility. They were able to respond to scarcity in numerous was including increasing leaf and arthropod consumption. They are therefore likely to be able to persist in fragmented Afromontane forest, even when other large bodied dispersers are going extinct. This means they are suitable candidates for investigation as surrogate dispersers. My conclusion on this matter are however unclear, largely due to including to broad a range of food items in analysis. *C. nititans* do however eat large amount of an array of large fruited species. They eat these regardless of availability. They also appear to respond to scarcity by altering overlap and niche width, however further work is needed into what species constitute the overlap. It would also be beneficial to compare overlap at greater range of availability levels, to see if the high overlap in 2013-2014 was a typical response or was instead a rare response to extreme scarcity. There is overall support for further research into *C. nictitans.* Curren data could be used to investigate overlap in fruit species and how the number of fruit species in the diet changes with food availability. It could also be used in conjunction with other data sets from other primates at Ngel Nyaki. For instance, determing the amount of overlap in *C. nictitans* and *Pan troglodytes ellioti.* If this was high it would help build a strong case for *C. nictitans* as a surrogate large bodied disperser. Future avenues of research include investigating diet in terms of nutritional content, *C. nictitans* may not be altering diet for food type but instead to keep a nutrient such as protein constant. This may explain the increase in arthropod consumption. Understanding nutrients and quality of different food types may help determine why and when *C. nictitans* diet varies, such as was seen in my study compared to most previous work. Also further research could be done on the diet of solo-males, as well as how diet and behaviour differs from troop males. Focusing on troops heavily biases data to female diet. Understanding how *C. nictitans* disperses seeds require knowledge of both sexes and both male lifestyles. Finally, I found that *C. nictitans* may in some circumstances favour fruit with large seeds, this requires further analysis. Most importantly seed characteristics must be consider in context of fruit characteristics to truly understand how *C. nictitans* are selecting fruit.s